

THE DEVELOPMENT AND ADULT STRUCTURE OF THE VERTEBRAL COLUMN IN *LEIOPELMA* (AMPHIBIA: ANURA)

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(Plates IX-XII)

Synopsis

The development of the vertebral column in an anuran with notochordal amphicoelous vertebrae, namely the rare, endemic New Zealand frog, *Leiopelma*, is described for the first time, and a detailed description is given of its internal morphology in adult stages. Long-standing claims that the persistent notochord and the absence of ball-and-socket joints in the vertebral column are primitive character-states in the Anura are upheld, contrary to a recent claim (Inger, 1967) that the ectochordal state of the vertebrae of *Leiopelma* has evolved secondarily as a result of neoteny from the holochordal condition found in most other frogs. All the so-called transverse processes of the vertebrae are pleurapophyses because discrete ribs are present during developmental stages, and the forked ribs of the third or fourth vertebrae enclose the anterior lymph hearts. The urostyle of *L. archeyi* develops from the first four pairs of postsacral neurapophyses and the ventral region of the perichordal tube of the first five postsacral vertebrae which undergoes squamous cell hyperplasia and subsequent metaplasia into hyaline cartilage to form the hypochord. Factors contributing to the evolution of the short presacral column and long pelvic girdle in anurans are also discussed.

Although it has been customary to place *Leiopelma* and the North American genus *Ascaphus* in the same family, differences in their vertebral morphology as well as a number of other characters strongly support Kuhn's (1967) suggestion that these two genera are not closely related. As *Leiopelma* and *Ascaphus* possess a number of character-states which are generally considered primitive in frogs, it would appear that they are both relics of ancient but otherwise independent groups within the Anura.

INTRODUCTION

Only two genera of living frogs, *Ascaphus* Stejneger, 1899 from North America and *Leiopelma* Fitzinger, 1861 from New Zealand, are known to possess notochordal amphicoelous vertebrae in adult stages. In other anurans the notochord is discontinuous if not entirely absent from the adult vertebral column and the joints between adjacent centra are synovial joints which may be procoelous, opisthocelous or amphicoelous in shape, the last-named having a free intervertebral disc. Various aspects of vertebral structure and development in anurans with synovial intercentral joints have been described by many authors, including Cope (1866), Gadow (1897, 1901, 1933), Ridewood (1897), Schauinsland (1906), Beddard (1907), Nicholls (1916), Gillies and Peberdy (1917), de Gaay Fortman (1918), Noble (1922, 1924, 1931), Mookerjee (1931), Ramaswami (1933), Zaharesco (1935), Mookerjee and Das (1939), Al-Hussaini (1941), Hodler (1949a, 1949b), Smit (1953), Stokely and List (1955) and de Silva (1956). Much of the earlier work on anuran vertebrae has been reviewed by Remane (1936), Devillers (1954) and Griffiths (1959a, 1963).

The only investigations concerned specifically with the vertebrae of ascaphids appear to be Ritland's (1955) account of the external and internal morphology of the adult vertebral column of *Ascaphus*, van Dijk's (1960) discussion of the number of vertebrae contributing to the urostyle in this genus and E. M.

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Stephenson's (1952, 1960) descriptions of the external features of the vertebrae of the three species of *Leiopelma*. There appears to be no detailed account, however, of the internal morphology of the adult vertebral column in *Leiopelma* or of vertebral development in either of these two genera.

The present investigation of the internal morphology and ontogenetic development of the vertebral column of *Leiopelma* has been undertaken in order to ascertain the extent to which it resembles the column of *Ascaphus* as described by Ritland (1955), and to determine if possible whether the ectochordal centra (*sensu* Griffiths, 1963) and uninterrupted notochord of adult stages are persistent ancestral conditions as believed by Noble (1924, 1931), E. M. Stephenson (1952), Griffiths (1963), Kluge and Farris (1969), Spinar (1972) and others or secondarily derived from the holochordal condition as postulated by Inger (1967).

MATERIAL AND METHODS

Twelve specimens of developing *Leiopelma archeyi* were available for investigation in the form of transverse, longitudinal or approximately horizontal serial sections cut at 10 or 12 μ and stained in van Gieson's stain, Masson's Trichrome or Heidenhain's Azan. As this material had already been sectioned, it was not possible to stage the embryos by reference to tables of development such as Shumway's (1940) table for *Rana pipiens* or Nieuwkoop and Faber's (1956) table for *Xenopus laevis*. They were therefore given the arbitrary stage numbers 2 to 9 to indicate increasing age. Stages 2 to 5 were intracapsular embryos, Stage 6 was hatching, while Stages 7, 8 and 9 were tailed froglets fixed one, two and three weeks after hatching respectively.

Five serially sectioned specimens of developing *Leiopelma hochstetteri* were also available, all cut transversely at 10 μ . They had been used in the experiments described by N. G. Stephenson (1955) and their ages with respect to hatching were unknown. As the youngest specimen of *L. hochstetteri* was clearly less advanced in its development than the youngest specimen of *L. archeyi*, it was called Stage 1, while two other specimens which appeared overall to be about the same age as the oldest *L. archeyi* were regarded as Stage 9H. These specimens were stained in Mallory's Triple Stain.

The adult material examined included a specimen of *L. archeyi*, male, snout-vent length 27 mm, and a specimen of *L. hochstetteri*, male, snout-vent length 34 mm. The vertebral columns of these two animals were serially sectioned horizontally at 10 μ and 12 μ respectively and stained in Mallory's Triple Stain and Masson's Trichrome.

Selected sections through developing and adult vertebrae were photographed using a Zeiss Photomicroscope II, while the vertebrae of *L. archeyi*, Stages 4, 6, 7, 8 and 9, are also illustrated by contour reconstructions using the method described by Pusey (1939). The magnification of all illustrations is shown by the accompanying horizontal or vertical line.

VERTEBRAL DEVELOPMENT

Leiopelma archeyi

Stage 2, T.S. (Pl. IX). The notochord is almost uniform in cross-sectional area throughout the trunk and is more dorsoventrally depressed anteriorly than posteriorly. There appears to be only one elastic notochordal sheath, contrary to Mookerjee's (1931) contention that a two-layered sheath is universal in the Anura, and the notochordal tissue itself is diffuse and vacuolated, the layer of cells underlying the notochordal sheath being the notochordal epithelium.

The relationships of the posterior region of the skull and the most anterior vertebra or atlas are not clear owing to the diffuse nature of the sclerotogenous mesenchyme in this region. Further posteriorly the neurapophyses are forming

between consecutive spinal nerve ganglia. The more anterior neurapophyses are cartilaginous while the more posterior elements are still procartilaginous. Each neurapophysis is dorsolaterally situated on the notochord, extending laterally to meet the myotome and dorsally as far as the ventral margins of the adjacent ganglia. Further dorsally beside each ganglion is an aggregation of mesenchymatous cells which are connected to the dorsal extremity of the neurapophysis, while the region dorsal to the ganglion between the spinal cord and the myotome is filled with loose mesenchyme. The surface of the notochord between and beneath the bases of the neurapophyses is invested by a thin layer of squamous cells which forms the perichordal tube.

Situated distally to the myotomes adjacent to the third vertebra are large vessels, the anterior lymph hearts, which at this stage are widely separated from the developing axial skeleton.

Stage 3, T.S. (Pl. IX, x). The notochord is oval and depressed in cross-section from the *basis cranii* to the tenth vertebra, gradually increasing in size posteriorly so that its cross-sectional area in the tenth vertebra is approximately four times that in atlas. Posterior to the tenth vertebra the notochord becomes cylindrical and even larger, so that its cross-sectional area in the anterior tail is approximately eight times that in atlas.

Fourteen pairs of neurapophyses are present. Their cartilaginous bases extend for a short distance anteriorly and posteriorly along the lateral surfaces of the perichordal tube in the anterior trunk and along its dorsolateral surfaces further posteriorly. The arch pedicels of the first twelve vertebrae are slender, subcylindrical structures curving around the spinal cord, and the procartilaginous apices of each pair of neurapophyses are widely separated from one another above the spinal cord. The arch pedicels of the thirteenth and fourteenth vertebrae extend only a short distance above the notochord to terminate laterally to the spinal cord. Cells from the dorsal extremities of the myotomes are contributing to the apices of the neurapophyses. A short distance below the apex of each neurapophysis of the second to the ninth vertebrae there are procartilaginous processes extending a short distance anteriorly and posteriorly from the arch. Only the posterior processes are present on the atlas and both pairs of processes are absent from the tenth and following vertebrae. These processes represent the developing zygapophyses and only those of the first three vertebrae are joined together by procartilage at this stage, those of the more posterior vertebrae being connected by diffuse bands of mesenchyme.

On the neurapophyses of the second to the tenth vertebrae there is a laterally directed transverse process whose apex is mesenchymatous. On some vertebrae, particularly the second, third, seventh and tenth, the unchondrified material is clearly a separate element from the transverse process and is therefore a rib, those of the third vertebra lying against the mesial surfaces of the anterior lymph hearts. Both transverse processes and ribs are lacking on atlas and vertebrae eleven to fourteen.

The perichordal tube of the first ten vertebrae has increased in thickness to become a sheath of squamous cells several cells thick, and is slightly thicker ventrally than dorsally to the notochord. Further posteriorly the outer limits of the perichordal tube are ill-defined, at first laterally then also ventrally to the notochord. In the regions between consecutive vertebrae the notochord is enclosed only by the perichordal tube, but between the atlantal neural arch and the occipital arch of the skull there are also strong cartilaginous connections attached to the lateral surfaces of the perichordal tube.

Occupying much of the space between consecutive neurapophyses at the level of the transverse processes are the ganglia of the spinal nerves. The only spinal nerve lacking a ganglion is the first, which lies between the atlantal arch and the skull and consists of the ventral root only. At this stage the ganglia

of nerves two to fourteen vary little in size, while those of the more posterior nerves gradually become smaller. The origins of the dorsal and ventral roots in the spinal cord are in almost the same transverse plane as the ganglia, and the spinal nerves pass ventrally on either side of the notochord.

Stage 4, late intracapsular embryo, L.S. (Fig. 1, Pl. x). The apices of the neurapophyses of the first ten vertebrae lie close together but have not fused, while those of the eleventh vertebra are still widely separated from one another. The arch pedicels are slender and subcylindrical and are orientated vertically to the notochord when seen in side view. The atlantal neural arch is the largest in the column and, dorsally to the spinal cord, is widely separated from the skull. The regional variation in the size of the neural arches and the notochord is illustrated in Fig. 1.

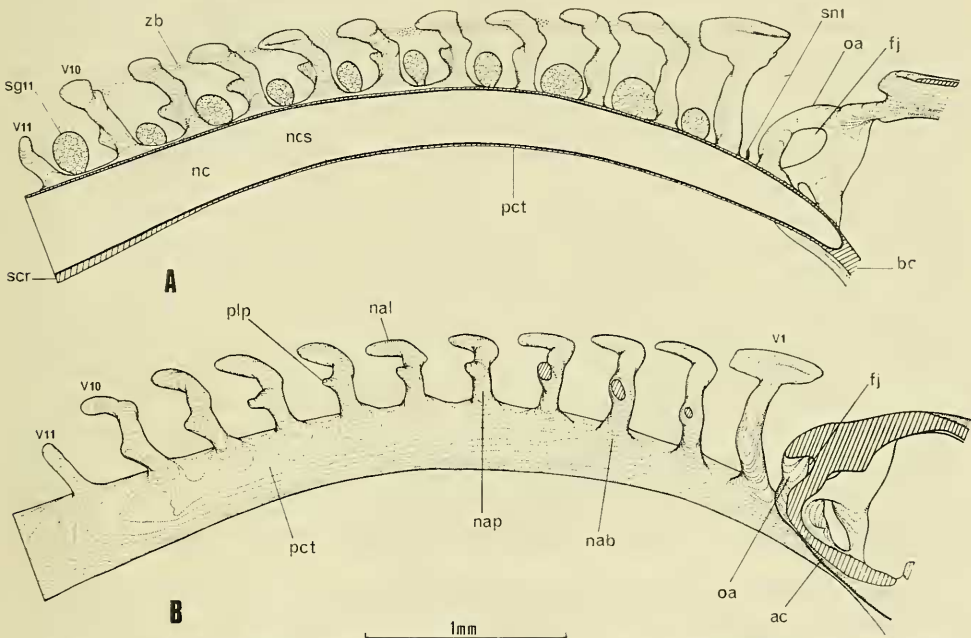


Fig. 1. Contour reconstructions of vertebrae 1-11 in a late intracapsular embryo (Stage 4) of *Leiopelma archeyi*. Posterior region of chondrocranium reconstructed in part. A. Medial view of half vertebral column showing relationship of procartilaginous zygapophyseal bars and spinal nerve ganglia to neural arches. B. Lateral view of vertebral column showing relationship of neural arches to perichordal tube. Ganglia and zygapophyseal bars omitted. *ac*, auditory capsule; *bc*, basis cranii; *fj*, foramen jugulare; *nab*, base of neural arch; *nal*, lamina of neural arch; *nap*, neural arch pedicel; *nc*, notochord; *ncs*, notochordal sheath; *oa*, occipital arch; *pct*, perichordal tube; *plp*, pleurapophysis; *scr*, subchordal rod; *sg11*, ganglion of 11th spinal nerve; *sn1*, 1st spinal nerve; *V1*, *V10*, *V11*, 1st, 10th and 11th vertebrae; *zb*, procartilaginous zygapophyseal bars.

All the neural arches as far back as the tenth vertebra are joined together by bands of procartilage lying dorsolaterally to the spinal cord and representing the zygapophyses. The zygapophyseal joints have not yet appeared, but the position of the atlanto-occipital joint is shown by a layer of younger cartilage which extends laterally and posteriorly from the surface of the notochord between the bases of the atlantal neural arch and the occipital region of the chondrocranium.

Regional variation has occurred in the sizes of the spinal nerve ganglia, the largest being those of nerves three, four and eleven, and the smallest those of nerves seven and eight.

The ventral part of the perichordal tube is of uniform thickness from the chondrocranium to the ninth vertebra but, from the tenth to the thirteenth vertebra its thickness ventrally to the notochord has increased owing to squamous cell hyperplasia.

Stage 5, later intracapsular embryo, T.S. and oblique H.S. (Pl. x). The notochord still has its greatest cross-sectional area in the anterior tail, in the twelfth and thirteenth vertebrae where it is almost circular in section. It gradually becomes smaller and more depressed in the more anterior vertebrae and posterior skull but further anteriorly in the *basis cranii* it is compressed slightly to become subcircular again in section. Posterior to the thirteenth vertebra the notochord tapers gradually to the end of the tail.

A sheath of squamous cells comprising the perichordal tube now invests the notochord throughout the vertebral column. It has chondrified by the deposition of matrix similar to that in the neural arches. In the specimen sectioned transversely the increase in thickness of the ventral part of the perichordal tube begins towards the posterior end of the tenth vertebra and reaches its maximum in the twelfth vertebra. In the thirteenth vertebra the thickness of the perichordal tube is reduced laterally to the notochord as well as ventrally so that the notochord of the fourteenth vertebra is invested by a uniformly thin sheath of squamous cells.

Fourteen pairs of neurapophyses are present, the first ten of which are fused together mid-dorsally. In contrast to the arch pedicels which are subcylindrical, the dorsal laminae of the arches are broader plates of cartilage which form a partial roof over the neural canal. The cartilaginous arch bases of the first nine vertebrae lie laterally to the notochord from which they are separated by the perichordal tube, and consecutive arch bases almost meet one another so that the intervertebral region is very short. In the tenth and following vertebrae the arches lie dorsolaterally to the notochord and the distance between consecutive arches increases. In this region, unlike the more anterior trunk, there is cartilaginous continuity between consecutive arch bases in the form of a band of cartilage attached to the dorsolateral surface of the perichordal tube. These tracts of cartilage extend posteriorly from the fourteenth pair of neurapophyses, varying slightly in thickness at irregular intervals. They are present as far back as the eighteenth pair of spinal nerves (Pl. x (F)), after which they diminish and disappear.

In the specimen sectioned transversely, only the second, third, fourth, tenth and eleventh vertebrae have clearly defined ribs, those of the second, third and fourth vertebrae being at least partly chondrified while those of the tenth and eleventh are mesenchymatous. There is no fusion in this specimen between the ribs of adjacent vertebrae.

In the specimen sectioned horizontally there are clearly defined ribs attached to the apices of the transverse processes of the third to the eleventh vertebrae inclusive. Those of the third, fourth and fifth vertebrae are cartilaginous, the right rib of the eighth vertebra is cartilaginous proximally and procartilaginous distally, while the remaining ribs consist entirely of procartilage. The right rib of the third vertebra is deeply notched to enclose the anterior lymph heart and is separate from the rib of the fourth vertebra. On the left side of the body the ribs of the third and fourth vertebrae are fused together and the combined rib encloses the lymph heart. In the posterior region of the body the largest rib elements are those of the tenth vertebra, suggesting that this is to be the sacral vertebra. At this stage, however, the ilia of the pelvic girdle are still widely separated from the vertebral column (Pl. x (F)).

Stage 6, at hatching, T.S. and L.S. (Figs 2, 3; Pl. XI). In the specimen sectioned transversely the cross-sectional area of the notochord gradually increases from front to back, reaching its maximum in the ninth, tenth and eleventh vertebrae, and there appears to be little change in its cross-sectional area

in the following two vertebrae. The notochord is laterally compressed to a small degree within the *basis cranii*, becoming circular in cross-section in the first three vertebrae. In the following eight vertebrae it is slightly depressed dorsoventrally while that of the more posterior tail is squarish in outline. In the specimen which was sectioned longitudinally, the notochord gradually increases in size from its anterior extremity just behind the hypophysis to the level of the fourteenth vertebra.

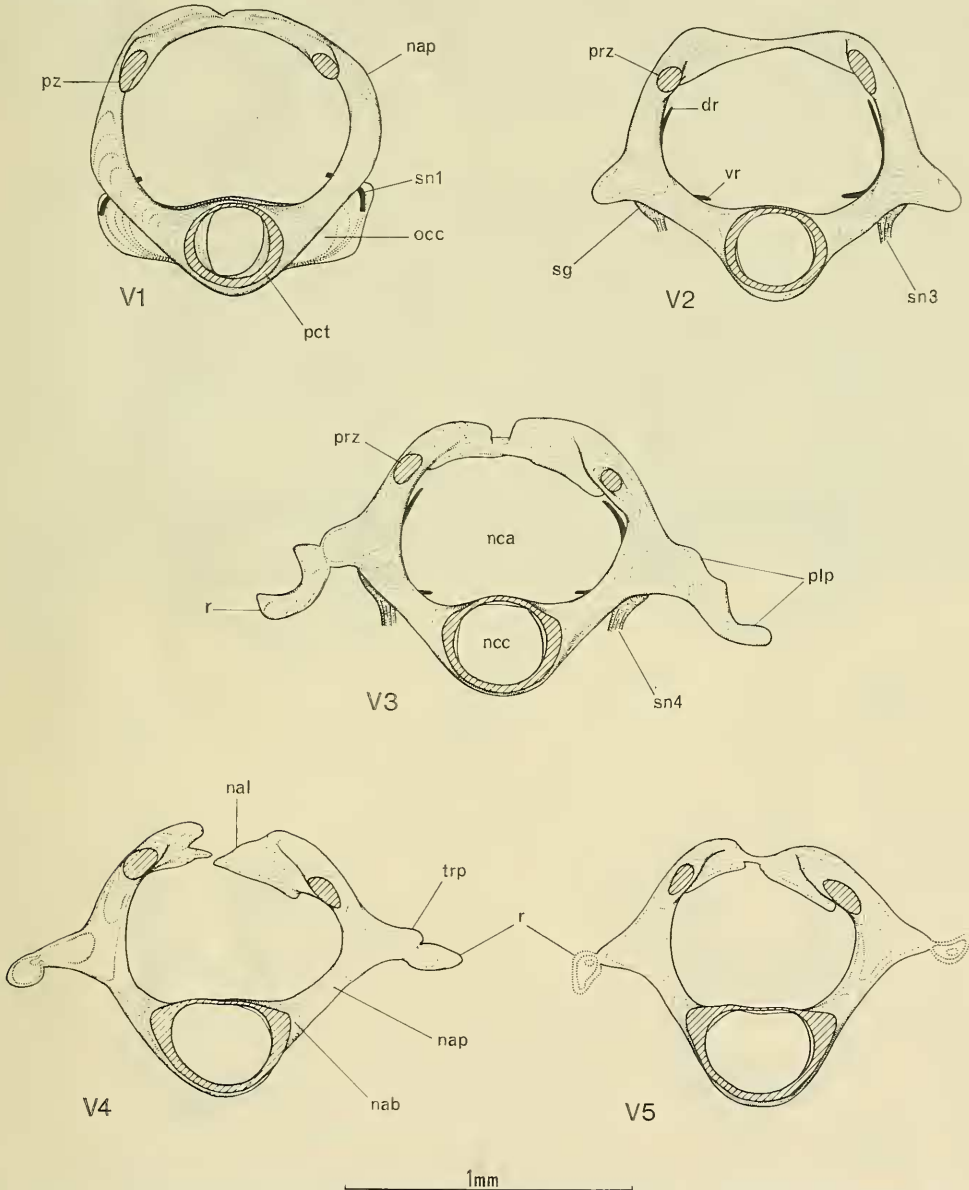


Fig. 2. Contour reconstructions of vertebrae 1-5 of *L. archeyi* at hatching (Stage 6). First vertebra from posterior aspect, vertebrae 2-5 in anterior view. The procartilaginous ribs of the 5th vertebra are shown in coarse stipple. *dr*, dorsal root of spinal nerve; *nab*, base of neural arch; *nal*, lamina of neural arch; *nap*, neural arch pedicel; *nca*, neural canal; *ncc*, notochordal canal; *occ*, occipital condyle; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis; *r*, rib; *sg*, spinal nerve ganglion; *sn1-4*, spinal nerves 1-4; *trp*, transverse process; *vr*, ventral root of spinal nerve.

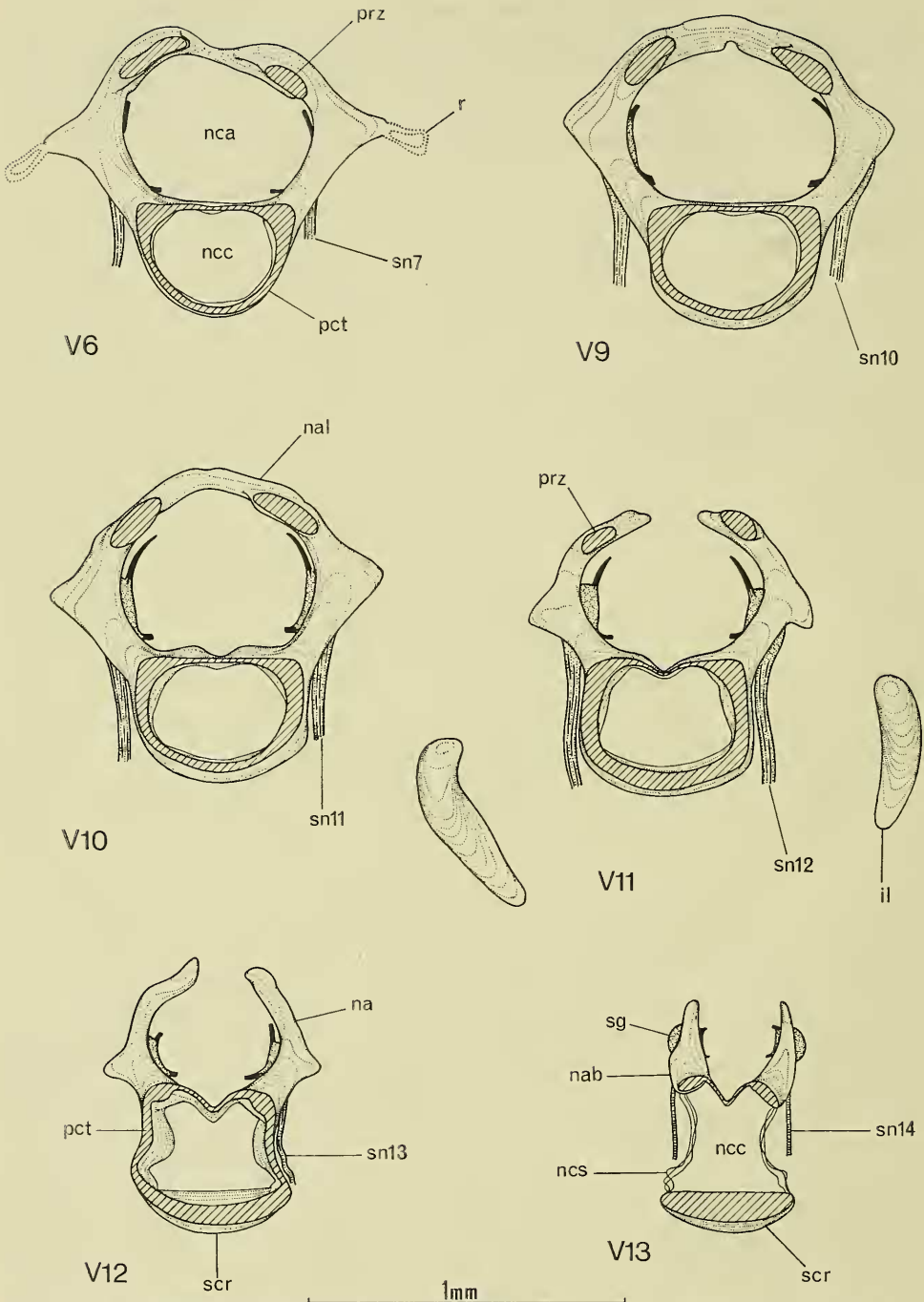


Fig. 3. Contour reconstructions from anterior aspect of the 6th vertebra and vertebrae 9-13 of *L. archeyi* at hatching (Stage 6). The procartilaginous ribs of the 6th vertebra are shown in coarse stipple. The mesenchymatous ribs of vertebrae 9-13 were too indistinct in outline for reconstruction. *il*, ilium; *na*, neural arch; *nab*, base of neural arch; *nal*, lamina of neural arch; *nca*, neural canal; *ncc*, notochordal canal; *ncs*, notochordal sheath; *pct*, perichordal tube; *prz*, prezygapophysis; *r*, rib; *scr*, subchordal rod; *sg*, ganglion of spinal nerve; *sn7-14*, spinal nerves 7-14.

The perichordal tube of the first ten vertebrae of both specimens is of uniform thickness along the vertebral column and is slightly thicker ventrally than it is dorsally to the notochord. The ventral thickening of the perichordal tube which begins at the posterior end of the tenth vertebra and reaches its maximum in the thirteenth vertebra is increased at this stage by the metaplasia of chondrified squamous cells into hyaline cartilage in which the cells are subspherical and the matrix more abundant. This subchordal rod of cartilage occupies the full width of the notochord and is chondrified as far as the posterior end of the thirteenth vertebra. The dorsal and lateral regions of the perichordal tube which lie between the arch bases and the subchordal rod of the thirteenth vertebra are thin and membranous. In the fourteenth vertebra the subchordal rod also becomes membranous and diffuse and disappears towards the posterior end of this vertebra.

In the specimen sectioned transversely, fourteen pairs of neurapophyses are present. Except for the fourth, and the eleventh to the fourteenth pairs, they are fused together dorsally to the spinal cord for a short distance near the posterior end of the arch. The arch bases of the first four vertebrae are attached laterally to the perichordal tube while those further posteriorly are more dorsolaterally placed with respect to the notochord. The tracts of cartilage extending back from the arch bases of the fourteenth vertebra disappear a short distance behind the vent at approximately the level of the sixteenth pair of spinal nerves so that the notochord in the remainder of the regressing tail is surrounded by a thin membranous perichordal tube. In the longitudinally sectioned specimen, none of the fourteen pairs of neurapophyses had fused together.

Transverse processes occur on all vertebrae with the exception of the atlas and the fourteenth vertebra, and in many cases have clearly defined rib elements attached to them. The ribs of the third vertebra are cartilaginous and are curved so that they lie against the mesial and ventral surfaces of the anterior lymph hearts, while those of the tenth vertebra are represented by condensations of mesenchyme attached to the transverse processes. At this stage the ilia are growing anteriorly and dorsally towards the vertebral column. Although the anterior ends of the ilia are level with the eleventh vertebra at this stage, the greater size of the tenth vertebra and its ribs than the eleventh vertebra and its ribs suggests that the former is the sacral vertebra. This is supported by the fact that the anterior ends of the ilia are procartilaginous and evidently in a state of rapid elongation.

The spatial relationships of the components of the spinal nerves with one another and the adjacent vertebrae are the same as in earlier stages: the dorsal and ventral nerve roots, the ganglia and the spinal nerves passing ventrally beside the vertebrae all lie in approximately the same transverse plane, and the ganglia lie in approximately the same horizontal plane as the transverse processes.

Stage 7, one week after hatching, T.S. and L.S. (Fig. 4). Although the two specimens representing this stage hatched and were fixed at the same time, the longitudinally sectioned specimen is more advanced in its vertebral development than the one sectioned transversely. As they also differ in other respects, they are described separately.

In the specimen sectioned transversely the notochord gradually increases in size posteriorly as far as the fifteenth vertebra. It is slightly compressed in the *basis cranii* and the first three vertebrae, is slightly depressed in the remaining vertebrae, and is somewhat irregular in cross-sectional outline. The perichordal tube is slightly thinner dorsally to the notochord than it is ventrally, while its lateral surfaces are covered by the cartilage of the neural arch bases except for a narrow region between adjacent vertebrae. The ventral thickening of the perichordal tube to form the subchordal rod begins in the tenth vertebra, has

partly changed into hyaline cartilage in the twelfth to the fourteenth vertebrae, and disappears in the region of the fifteenth vertebra between the fifteenth and sixteenth pairs of spinal nerves.

Fifteen pairs of neurapophyses are present in this specimen, the more anterior eleven of which are fused together mid-dorsally. The neurapophyses of the twelfth vertebra lie close together above the spinal cord without fusing while those of the thirteenth, fourteenth and fifteenth vertebrae consist of the arch pedicels only, and these diminish in size posteriorly. Joint cavities are forming in the cartilaginous zygapophyseal bars connecting the first three vertebrae, those connecting the third to the eleventh vertebrae being undivided although the position of the joint is clearly defined. Posterior to the eleventh vertebra there are no zygapophyseal connections between consecutive neural arches.

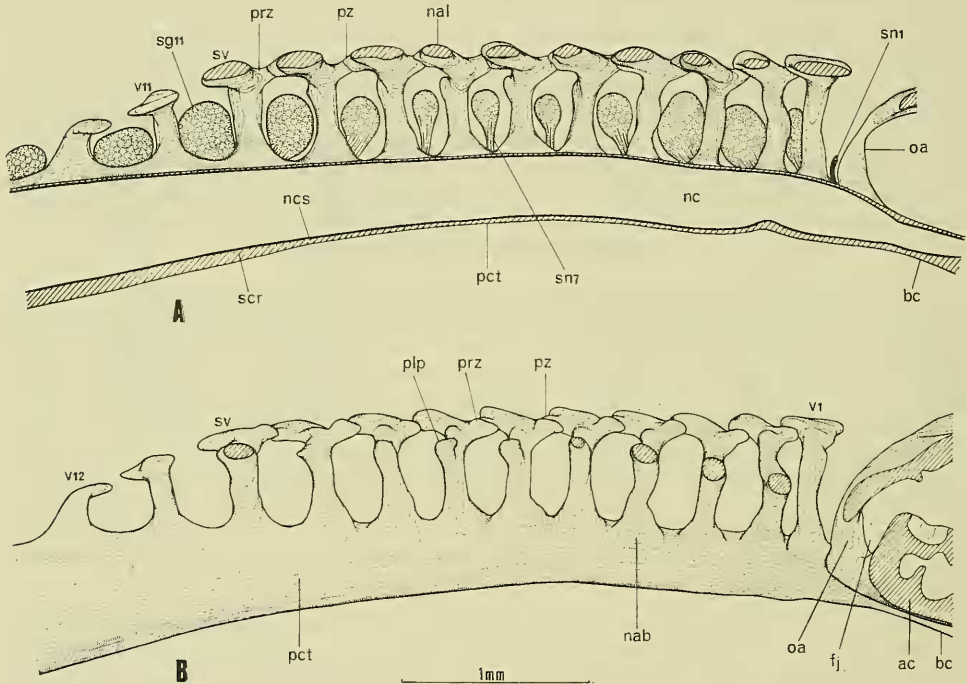


Fig. 4. Contour reconstructions of vertebrae 1-12 of *L. archeyi* one week after hatching (Stage 7). Posterior region of chondrocranium reconstructed in part. A. Medial view of half vertebral column showing relationship of neural arches to one another and to ganglia of spinal nerves. B. Lateral view of vertebral column showing relationship of neural arches to one another and to perichordal tube. Ganglia omitted. ac, auditory capsule; bc, basis cranii; fj, foramen jugulare; nab, base of neural arch; nal, lamina of neural arch; nc, notochord; ncs, notochordal sheath; oa, occipital arch; pct, perichordal tube; plp, pleurapophysis; prz, prezygapophysis; pz, postzygapophysis; scr, subchordal rod; sg11, ganglion of 11th spinal nerve; sn1, sn7, 1st and 7th spinal nerves; sv, sacral vertebra; V1, V11, V12, 1st, 11th and 12th vertebrae.

Transverse processes are present on all vertebrae except the atlas and the last three in the column. Cartilaginous ribs are attached to the transverse processes of the third, fourth and fifth vertebrae, those of the fourth vertebra instead of the third as is usual in *Leiopelma* being deeply notched to enclose the anterior lymph hearts. The ribs associated with the sixth, seventh and twelfth vertebrae are procartilaginous or mesenchymatous while the remaining vertebrae lack separate rib elements. The pleurapophyses of the eleventh vertebra are

connected to the ilia of the pelvic girdle by broad bands of connective tissue, thus demonstrating that the eleventh vertebra is the sacral vertebra in this specimen instead of the tenth as is usual in *Leiopelma* (E. M. Stephenson, 1952, 1960).

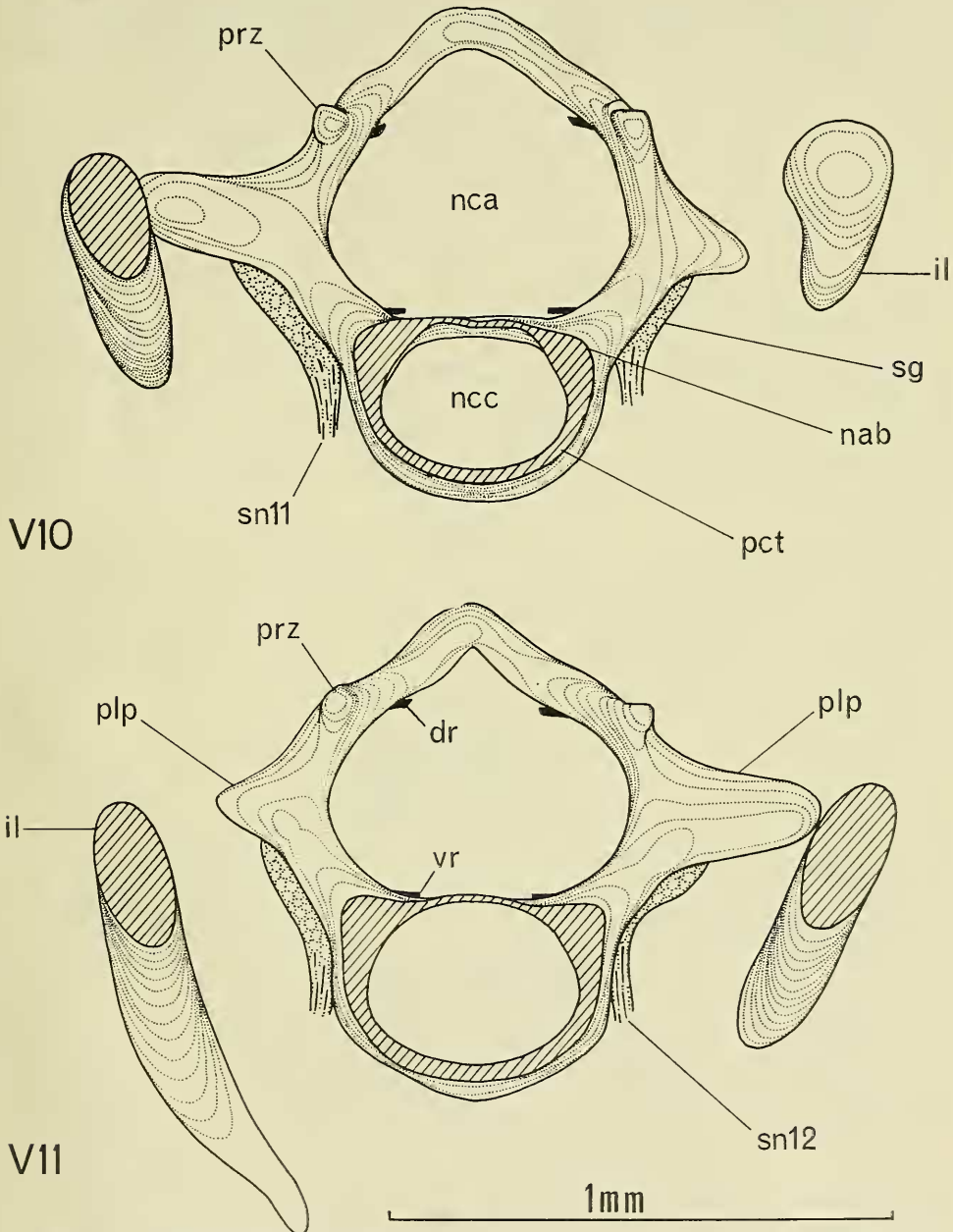


Fig. 5. Anomalous sacrum comprising the 10th and 11th vertebrae in a specimen of *L. archeyi* two weeks after hatching (Stage 8). Contour reconstructions from anterior aspect. *dr*, dorsal root of spinal nerve; *il*, ilium; *nab*, base of neural arch; *nca*, neural canal; *ncc*, notochordal canal; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *sg*, ganglion of spinal nerve; *sn11*, *sn12*, 11th and 12th spinal nerves; *vr*, ventral root of spinal nerve.

A synovial cavity has begun to form in the posterolateral regions of the atlanto-occipital joint, the more medial region of the joint on either side of the continuous notochord remaining undivided.

In the specimen which was sectioned longitudinally, the tenth vertebra is the sacral vertebra, a total of fourteen pairs of neurapophyses are present, the first ten of which are fused together mid-dorsally, and the ribs of the third vertebra are notched to enclose the anterior lymph hearts. The somewhat more advanced

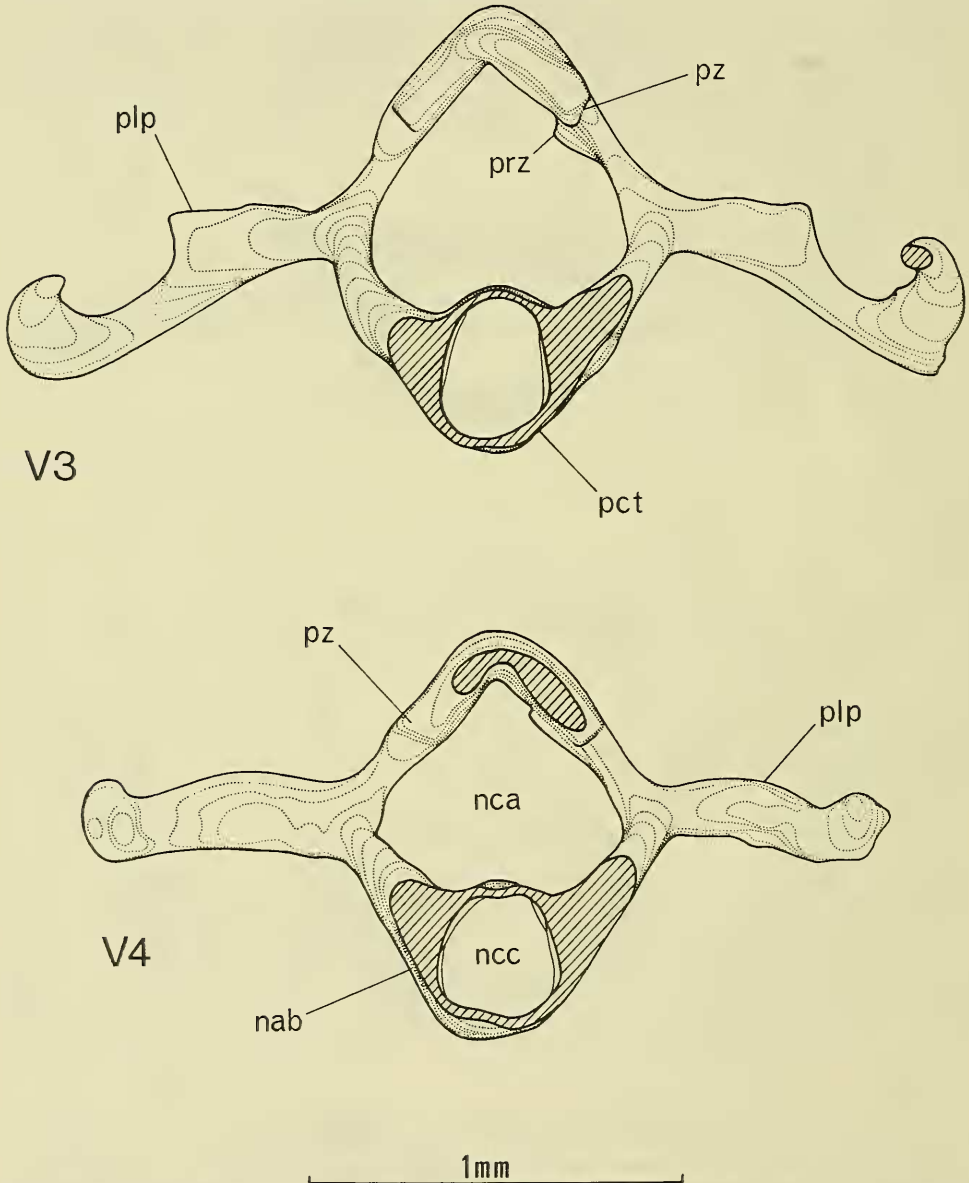


Fig. 6. Third and fourth vertebrae of *L. archeyi* three weeks after hatching (Stage 9). Contour reconstructions from posterior aspect. *nab*, base of neural arch; *nca*, neural canal; *ncc*, notochordal canal; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis.

state of vertebral development in this specimen is shown by the presence of joint cavities in all the zygapophyseal bars connecting the first ten vertebrae, there being no zygapophyseal connections between the more posterior neural arches, the somewhat greater extent of the synovial cavity in the atlanto-occipital joint, and the onset of perichondral ossification of the vertebrae. Ossification begins on the neural arches at the level of the transverse processes but does not extend to the ends of these processes or to the bases or the laminae of the arches.

Stage 8, two weeks after hatching, T.S. (Fig. 5). Perichondral ossification of the vertebrae is more advanced than in Stage 7, extending further down the neural arches towards their bases and further dorsally onto the arch laminae. The synovial cavities between the zygapophyses are more extensive with the postzygapophyses overlying the prezygapophyses of the following vertebrae. The neurapophyses of the eleventh vertebra as well as those of the more anterior vertebrae are fused together mid-dorsally.

Of the two specimens at this stage which were available for investigation, one had fourteen and the other fifteen pairs of neurapophyses. In the latter, the sacrum is anomalous in that the right transverse process of the tenth vertebra and the left process of the eleventh vertebra support the pelvic girdle (Fig. 5). In the former the sacrum appears to consist of only the tenth vertebra but, unlike the latter in which the transverse processes supporting the girdle are in contact with the ilia, the transverse processes and ilia of this specimen are widely separated from one another. It would thus appear that this specimen is also anomalous in that development of the sacrum has been retarded relative to the rest of the column.

Stage 9, three weeks after hatching, T.S. (Figs 6, 7; Pls XI, XII). There are fourteen pairs of neurapophyses of which the first twelve are fused together mid-dorsally, the thirteenth are widely separated dorsally to the spinal cord and the fourteenth consist of low arch pedicels. Further posteriorly the bars of cartilage lying along the dorsolateral surfaces of the perichordal tube are irregularly thickened and end just behind the sixteenth pair of spinal nerves. At this stage there is cartilaginous continuity between all the neural arch bases on each side of the body as a result of fusion between consecutive arches on the dorsolateral surface of the perichordal tube. The perichordal tube itself has the same configuration in the presacral region as it did in Stage 7.

The notochord is slightly compressed from side to side in the *basis cranii*, the nine presacral vertebrae and the anterior end of the tenth or sacral vertebra, increasing gradually in cross-sectional area from front to back. Within the posterior end of the sacral vertebra the cross-sectional area of the notochord is suddenly reduced to less than half its value at the anterior end of the vertebra as a result of centripetal growth of the neural arch bases and subchordal rod. Maximum constriction of the notochord occurs in the twelfth vertebra behind which it gradually expands to become only slightly smaller at the end of the subchordal rod than in the anterior end of the sacral vertebra. Within this region of notochordal constriction the appearance of the notochordal sheath and notochordal tissue also change, the sheath being corrugated and thickened due to constriction, and the notochordal tissue more dense due to an accumulation of non-cellular material. In the presacral vertebrae and in the tail posterior to the end of the subchordal rod, the notochord and its sheath appear the same histologically as at the onset of vertebral development.

The subchordal rod is now composed entirely of hyaline cartilage and gradually narrows from the posterior end of the sacral vertebra to its posterior end just behind the vent, at the level of the sixteenth pair of spinal nerves.

In the eleventh and twelfth vertebrae the subchordal rod has fused on either side of the notochord to the ventral surfaces of the neural arch bases while the arch bases of the thirteenth and fourteenth vertebrae and the following bars of

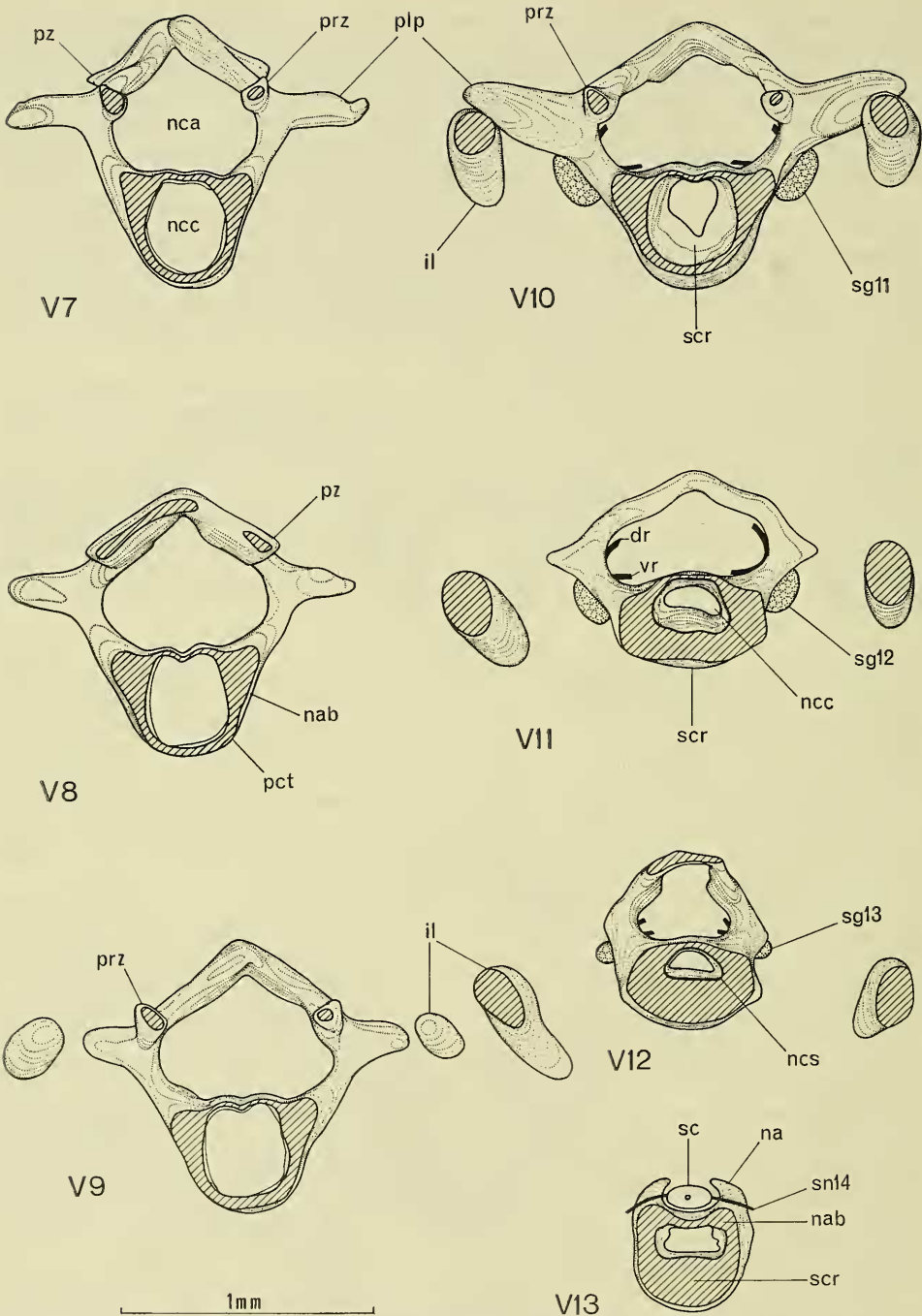


Fig. 7. Contour reconstructions of vertebrae 7-13 in *L. archeyi* three weeks after hatching (Stage 9). 8th and 13th vertebrae in posterior view, remainder from anterior aspect. *dr*, dorsal root of spinal nerve; *il*, ilium; *na*, neural arch; *nab*, base of neural arch; *nca*, neural canal; *ncc*, notochordal canal; *ncs*, notochordal sheath; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis; *sc*, spinal cord; *scr*, subchordal rod; *sg11-13*, ganglia of spinal nerves 11-13; *sn14*, 14th spinal nerve; *vr*, ventral root of spinal nerve.

cartilage are still separated from one another and the subchordal rod by the perichordal tube. In the region of the tail posterior to the end of the subchordal rod the perichordal tube is of almost uniform thickness around the notochord and is apparently fibrous in nature.

Synovial joints are present between the postzygapophyses of the first to the ninth vertebrae and the prezygapophyses of the second to the tenth vertebrae, posterior to which there are no zygapophyses. Their articular surfaces are flat in end view and are inclined upwards and outwards from the midline at an angle of approximately 45° to the horizontal. The synovial joint between atlas and the occipital condyles is not yet complete and is traversed by the unconstricted notochord.

There are no discrete rib elements present at this stage owing to their fusion to the transverse processes of the vertebrae. As discrete ribs have been found at some stage of development in association with all vertebrae bearing transverse processes, the latter are more correctly described as pleurapophyses. The pleurapophyses of the third vertebra are deeply notched to enclose the anterior lymph hearts which are covered dorsally by the cartilaginous suprascapulae of the pectoral girdle. The pleurapophyses of the tenth or sacral vertebra lie dorsally to the ilia of the pelvic girdle, to which they are attached by ligaments. The ilia extend anteriorly beyond this point to reach the level of the pleurapophyses of the ninth vertebra but are not joined to them.

The spinal ganglia are more ventral in position at this stage, lying between the pedicels of the neural arches below the level of the pleurapophyses. The relative positions of the dorsal and ventral nerve roots, the ganglia and the spinal nerve trunks are also changing in different parts of the body. The result is that the nerve roots, particularly towards the sacrum, come to lie some distance anteriorly to the ganglia to which they belong. The relationship of the nerves to the vertebrae is described below in the section on adult stages. Sixteen pairs of spinal nerves are present at this stage, the most posterior of which lie laterally to the posterior end of the subchordal rod.

Leiopelma hochstetteri

Stage 1, T.S. In this specimen, the youngest of all the available specimens of *Leiopelma*, the spinal cord is flanked dorsolaterally by the neural crest and laterally by the somites which have not yet begun to differentiate into myotomes and sclerotomes. The notochord lying between the spinal cord and the subnotochord has a single sheath and the same histological characteristics as in *L. archeyi*.

Stage 9H, T.S. Of the two oldest available specimens of *L. hochstetteri*, one was sectioned completely and the other only as far back as the anterior end of the eighth vertebra. These two specimens are a little more advanced than the oldest available specimen of *L. archeyi* (Stage 9) with respect to perichondral ossification in that the layer of bone on the neural arches is somewhat thicker and extends further dorsally towards the apices and further ventrally towards the bases of the neurapophyses. The transverse processes have also ossified as far as their junction with the associated ribs.

In some other respects, vertebral development in these specimens of *L. hochstetteri* is less advanced than in *L. archeyi* Stage 9. In the partially sectioned specimen the first four pairs of neurapophyses are unfused while in the other specimen, which has thirteen pairs of neurapophyses in all, the apices of the first ten pairs lie close together above the spinal cord but remain unfused. The eleventh, twelfth and thirteenth pairs of arches are more widely separated mid-dorsally. Ribs are still detectable as distinct elements from the transverse processes of the vertebrae, those of the third and fourth vertebrae being cartilaginous and fused to the transverse processes. The more posterior ribs are

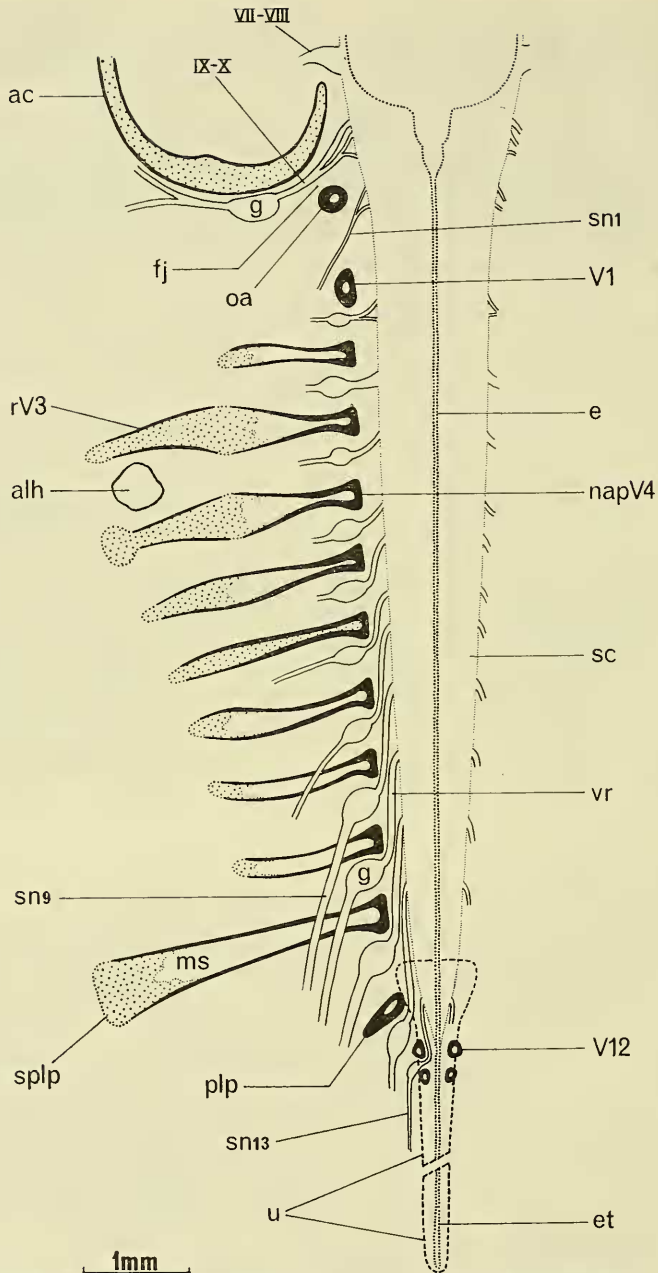


Fig. 8. Composite horizontal section of vertebral column and posterior skull of adult *L. archeyi* in ventral view, showing relationship of spinal nerves, ganglia and ventral nerve roots to spinal cord, neural arches and urostyle. As the urostyle lies ventrally to the ependymal tube, its position is indicated by a heavy broken line. Only the anterior and posterior ends of the urostyle are shown. Diagrammatic, scale approximate. *ac*, auditory capsule; *alh*, anterior lymph heart; *e*, ependyma; *et*, ependymal tube; *fj*, foramen jugulare; *g*, ganglion; *ms*, marrow space; *napV4*, neural arch pedicel of 4th vertebra; *oa*, occipital arch; *plp*, pleurapophysis; *rV3*, rib of 3rd vertebra; *sc*, spinal cord; *sn1*, *sn9*, *sn13*, 1st, 9th and 13th spinal nerves; *splp*, sacral pleurapophysis; *u*, urostyle; *V1*, *V12*, 1st and 12th vertebrae; *vr*, ventral nerve root; *VII-X*, cranial nerves. Bone, solid black; cartilage, coarse stipple.

procartilaginous or mesenchymatous, including the ribs of the tenth vertebra, which appears by virtue of its size to be the sacral vertebra although it is still widely separated from the ilia of the pelvic girdle. There is slight constriction of the notochord within the eleventh and twelfth vertebrae but its histological appearance remains unchanged. The subchordal rod consists of hyaline cartilage for the greater part of its length but it has not yet fused to the bases of the post-sacral neural arches.

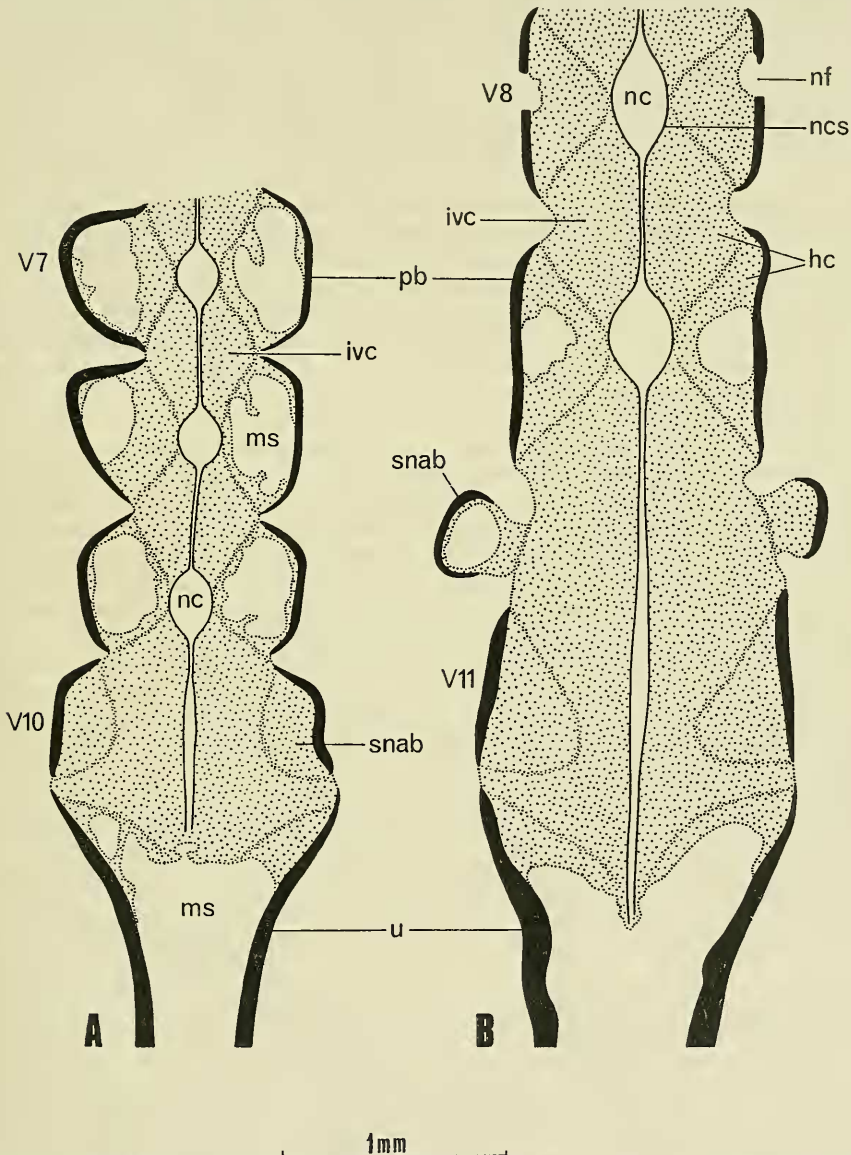


Fig. 9. Posterior vertebrae and anterior end of urostyle of adult *Leiopelma* in horizontal section showing the structure of the sacral vertebra and the relationships between the notochord, the bases of the neural arches and the intervertebral cartilage. A. *L. archeyi*, ♂, snout-vent length 27 mm. B. *L. hochstetteri*, ♂, snout-vent length 34 mm. *hc*, hyaline cartilage; *ivc*, intervertebral cartilage; *ms*, marrow space; *nc*, notochord; *ncs*, notochordal sheath; *nf*, nutritive foramen; *pb*, perichondral bone; *snab*, base of sacral neural arch; *u*, urostyle; V7-V11, 7th to 11th vertebrae.

With respect to the joints developing between atlas and the occipital condyles and between the zygapophyses of consecutive vertebrae, these two specimens of *L. hochstetteri* are comparable with the Stage 9 specimen of *L. archeyi*.

ADULT VERTEBRAL COLUMN

L. archeyi, H.S. (Figs 8, 9; Pl. XII). Thirteen pairs of neurapophyses are present in this specimen, of which the first nine are presacral, the tenth is sacral, and the eleventh, twelfth and thirteenth are fused to the anterior dorsal surface of the urostyle. The first eleven pairs of arches are fused together mid-dorsally and, with the exception of the sacral vertebra, the perichondral bone of the arch laminae is fused as well as the inner core of hyaline cartilage. The neural arch of the sacral vertebra remains unossified mid-dorsally. The arches of the twelfth and thirteenth vertebrae are separate mid-dorsally but fused together on either side of the neural canal dorsally and ventrally to the thirteenth pair of spinal nerves. The arches of the first ten vertebrae articulate by means of zygapophyses and are also connected by strong sheets of collagenous connective tissue. A similar connective tissue sheet joins the atlantal arch to the occipital arch of the skull but there is no zygapophyseal connection between these two arches which are widely separated from one another. Zygapophyses are also absent posterior to the sacrum. The tenth and eleventh arches are widely separated and the eleventh, twelfth and thirteenth arches are considerably smaller than those of the more anterior vertebrae.

With the exception of atlas and the twelfth and thirteenth vertebrae, all the neural arches bear pleurapophyses, those of the presacral and sacral vertebrae being ossified perichondrally for the greater part of their length and cartilaginous at their distal extremities. Most of them have also undergone endochondral ossification but the marrow spaces do not extend as far distally as the layer of perichondral bone so that the ends of the processes retain a core of hyaline cartilage. In those pleurapophyses with a suture in the perichondral bone between the rib element and the transverse process, namely those of the third and fourth vertebrae, the marrow cavities do not extend out beyond the level of the sutures. In each case, endochondral ossification of the pleurapophyses appears to have progressed outwards from the neural arch rather than originating from separate ossification centres within the pleurapophyses. The pleurapophyses of the eleventh vertebra are much smaller than those of the more anterior vertebrae and consist almost entirely of perichondral bone.

From the occiput to the twelfth vertebra the neural canal enclosed by the neural arches contains the spinal cord, which tapers gradually posteriorly as it gives off successive spinal nerves of which there are thirteen pairs in all. The spinal cord itself does not extend further posteriorly than the twelfth vertebra, but its investing membranes and the lining of the spinal canal or ependyma continue back between the thirteenth pair of neurapophyses and along the dorsal surface of the urostyle to its posterior extremity. The most anterior spinal nerve on each side has neither ganglion nor dorsal root, but its ventral root is in two parts lying close together, one behind the other. The following twelve pairs of nerves have dorsal and ventral roots as well as ganglia although the ventral roots of the second pair resemble those of the first in having two components arising from the spinal cord. The roots and ganglia of the third pair of nerves lie in approximately the same transverse plane, but further posteriorly the distance between the origins of the nerve roots in the spinal cord and the ganglia to which they belong becomes greatly increased. Maximum displacement is found in the case of the eleventh nerve, whose ganglion lies between the tenth and eleventh vertebrae and whose roots leave the spinal cord anteriorly to the ninth vertebra.

The bodies of the presacral and sacral vertebrae, often referred to as centra, are largely cartilaginous, the only bone present being the perichondral and

endochondral bone of the neural arch bases, which extend almost to the ventral surface of the column, and the thin layer of perichondral bone covering the dorsal and ventral surfaces of the vertebral bodies. All the cartilage within and between consecutive vertebrae is hyaline cartilage, the perichordal tube of chondrified squamous cells present in developmental stages having disappeared. From the arrangement of the cartilage cells and matrix within the vertebrae, which is more clearly seen in the specimen of *L. hochstetteri* than in this specimen of *L. archeyi*, it is evident that much of the cartilage of the presacral vertebral bodies belongs to the bases of the neurapophyses. The cartilage between adjacent vertebrae appears to have arisen as a result of hyperplasia of the perichordal tube in the ends of adjacent vertebral bodies which has become hyaline like the arch bases. Unlike the neural arch bases, however, whose growth has not constricted the notochord to any extent, growth of the cartilage in the ends of the vertebrae has constricted the notochord to a slender thread.

The notochord, together with its sheath, is still continuous from the posterior region of the *basis cranii* to the anterior end of the urostyle ventral to the eleventh pair of neurapophyses. It is continuous through the atlanto-occipital joint, lying very close to the ventral surface of the joint, and contains fibrous cartilage in the base of the skull, the joint region and the anterior end of atlas. In the middle of atlas, as in the following eight vertebrae, it is unconstricted and extends almost to the dorsal and ventral surfaces of each vertebral body. In these vertebrae it has essentially the same histological appearance as in earlier stages. In the sacral vertebra the notochord is constricted to a considerable extent and has changed histologically to appear fibrous and non-cellular. In this form and with little further constriction the notochord passes back into the anterior end of the urostyle, but it terminates here owing to the presence of the adjacent marrow space. No vestige of the notochord remains further posteriorly; the urostyle has ossified perichondrally and endochondrally for almost its entire length, the single cavity within it being a marrow space in endochondral bone, not the notochordal canal. The only parts of the urostyle which are still cartilaginous are the most anterior portion of the urostyle where it joins the body of the sacral vertebra and its most posterior extremity where it still appears to be growing.

L. hochstetteri, H.S. (Fig. 9; Pl. XII). Of the thirteen neural arches present in this specimen the tenth is sacral, the eleventh belongs to an additional post-sacral vertebra, and the twelfth and thirteenth are fused to the anterior end of the urostyle. Zygapophyseal joints connect the first to the eleventh arches, there being no zygapophyseal connections between the atlantal arch and the occipital arch of the skull or between the arches posterior to the eleventh vertebra. The two halves of the first twelve arches are joined together mid-dorsally by hyaline cartilage which, except for that of the tenth vertebra, is enclosed in a thin layer of perichondral bone, while the two halves of the thirteenth arch are separate from one another.

Pleurapophyses are borne by the second to the twelfth vertebrae inclusively, those of the presacral and sacral vertebrae possessing cartilaginous distal portions which, except for those of the ninth vertebra, are fused to their transverse processes. The distal cartilaginous rib elements of the ninth vertebra are connected to their transverse processes by ligaments. The bases of the pleurapophyses contain marrow spaces continuous with those in the neural arches but in the pleurapophyses of the third and fourth vertebrae which have sutures in their perichondral bone, the marrow spaces do not extend into the ribs. The pleurapophyses of the eleventh and twelfth vertebrae are ossified to the tip.

As in *L. archeyi*, there are thirteen pairs of spinal nerves, of which only the first pair lacks dorsal roots and ganglia. The relationship of the nerves to their

roots and ganglia and to the spinal cord, and the transition from spinal cord to ependymal tube in the region of the twelfth neural arch are also similar in the two specimens.

Except for the sacral and immediately postsacral regions, the relationships of the neural arch bases to the intervertebral cartilage and the internal structure of the vertebral bodies including the conformation of the notochord are the same in *L. hochstetteri* as in *L. archeyi*. The similarities and differences between these two frogs in the structure of their posterior presacral, sacral and postsacral vertebrae are illustrated in Fig. 9. The body of the sacral vertebra in both cases consists in part of the bases of the neural arches but, unlike the presacral vertebrae, the mesial surfaces of the arch cartilages do not lie close to the surface of the notochordal sheath. These elements are separated from one another by a region of cartilage which is hyaline like that of the arch bases but which appears, like the hyaline intervertebral cartilage, to have formed as a result of metaplasia and hyperplasia of the perichordal tube. Like the intervertebral cartilage also, and unlike the cartilages of the arch bases, the cartilaginous core of the sacral vertebra has strongly constricted the notochord within it. In *L. archeyi* the bases of the sacral neural arches contribute to the body of the vertebra, but in *L. hochstetteri* the arches are separate from the dorsal regions of the vertebral body, and further ventrally where they join the latter they project laterally from the surface of the column. In both frogs the sacral neural arches are smaller in horizontal section than those of the presacral vertebrae, and are proportionally much smaller in *L. hochstetteri* than in *L. archeyi*.

DISCUSSION

From the foregoing description of the development and adult structure of the vertebral column of *Leiopelma archeyi* and *L. hochstetteri* as well as from E. M. Stephenson's (1952, 1960) accounts of the external morphology of the vertebrae of all three species of *Leiopelma*, it is evident that individual variation in vertebral characteristics is not uncommon. Embryos of the same age may be at somewhat different stages of vertebral development as shown by the closure or otherwise of the neurapophyses, the proximity of the ilia of the pelvic girdle to the vertebral column and the extent of perichondral ossification while the structure of the column can also vary in the number of presacral vertebrae (nine or ten), the number of vertebrae modified to support the ilia and the number of postsacral vertebrae which are free or are incorporated into the anterior end of the urostyle. Variation also occurs in the ribs of the more anterior vertebrae in that those of the third, fourth or both may be forked, and fusion can occur between these ribs on either side of the body. As this range of variability was observed in the comparatively few specimens available for the present investigation, it is often difficult to be certain which embryonic and adult features are characteristic of species and which are due to individual variation. Also some developmental stages were not represented, notably the early intracapsular stage between Stages 1 and 2 exhibiting the sclerotomic precursors of the vertebrae, and sub-adult stages more than three weeks old. Consequently it was not possible to determine the cellular density of the sclerotomes or the presence or absence of a sclerocoel (see Wake, 1970). Nor was it possible to observe the onset of endochondral ossification in the neural arches, or ossification of the perichordal tube as illustrated in *L. hochstetteri* by E. M. Stephenson (1960), or later stages in the formation of the cranio-vertebral joint and urostyle, which apparently occur after the completion of metamorphosis. Despite these limitations, however, it is possible to compare the adult vertebral columns of *Leiopelma* and *Ascaphus* with one another and with non-ascaphid anurans as well as a number of features of vertebral development in *Leiopelma* and non-ascaphids.

Vertebral Column of Adult Leiopelma and Ascaphus

Leiopelma and *Ascaphus* are unique among living anurans in that they retain an uninterrupted notochord and lack synovial joints between the bodies of adjacent vertebrae throughout life (E. M. Stephenson, 1952, 1960; Ritland, 1955). Although some other frogs such as *Rana temporaria* retain these characteristics for some two years after metamorphosis, synovial cavities form during the third year and the notochord is subsequently entirely lost from the ends of the vertebrae (Mookerjee, 1931). In Griffiths' (1963) terminology, the vertebrae of *Leiopelma* and *Ascaphus* are ectochordal in that the fully formed vertebral body is a hollow bony cylinder enclosing the persistent notochord while the vertebrae of *Rana* are holochordal because the notochord is ultimately resorbed so that the body of the vertebra becomes a solid cylinder of bone. The term amphicoelous has also been used to describe the vertebrae of *Ascaphus* and *Leiopelma* but its accuracy has been questioned by E. M. Stephenson (1952, 1960) and Ritland (1955) on the grounds that the vertebrae of these frogs are structurally very different from the notochordal amphicoelous vertebrae of some other vertebrates.

In *Leiopelma* the bodies of adult presacral vertebrae consist of the perichordal tube together with the bases of the neural arches which cover its lateral surfaces. Although Ritland (1955) described the laterally situated endochondrally ossified regions of the vertebral bodies in *Ascaphus* as centra, a comparison between his illustrations of the vertebrae in end view with his horizontal sections shows that these ossified regions are the arch bases as in *Leiopelma*. In both genera the notochord is moniliform in shape and its extreme constriction between consecutive vertebrae results from hyperplasia of the perichordal tube in this region to form the intervertebral cartilage. Although the mid-vertebral regions of the notochord appear unconstricted, a comparison between the width of the notochord in the eighth and ninth vertebrae of a tailed froglet of *L. archeyi* three weeks after hatching (Fig. 7) and that in a sexually mature specimen (Fig. 9) shows that some mid-vertebral constriction occurs as well.

Despite the overall similarity between *Leiopelma* and *Ascaphus* in the internal morphology of their presacral vertebrae, there are also differences between them. The neural arch bases of *Ascaphus* (Ritland, 1955, Fig. 3, Pl. 1) contain considerably more endochondral bone than those of *Leiopelma* (Fig. 9) including *L. hochstetteri* which, according to E. M. Stephenson (1960), has the most heavily ossified skeleton of all three species of *Leiopelma*. The notochord, on the other hand, is more strongly constricted intervertebrally in *Leiopelma* than in *Ascaphus* and differs histologically in the two genera. In *Leiopelma* the notochord is fibrous only where it is strongly constricted between consecutive vertebrae, the tissue within the unconstricted mid-vertebral portions consisting of vacuolated notochordal cells, but in *Ascaphus* the fibrous cord is continuous throughout the vertebral column, forming a fibrous core through the middle of the vacuolated notochordal tissue in the centre of each vertebra.

Primitiveness of Ectochordy and Continuous Notochord

Until recently it was generally accepted that the ectochordal centra and continuous notochord in *Ascaphus* and *Leiopelma* are ancestral conditions retained in living forms (Noble, 1924, 1931; E. M. Stephenson, 1952; Griffiths, 1963; Kluge and Farris, 1969; Spinar, 1972). Inger (1967), however, postulated that ectochordal centra have been secondarily derived from the holochordal condition as a result of neoteny. He pointed out the reduced ossification of the skeleton in some species of ascaphids, namely of *Leiopelma* as described by E. M. Stephenson (1960), and considered the holochordal condition to be primitive

because most lepospondylous amphibians had holochordal vertebrae. According to Inger, the only evidence for the primitive nature of ectochordy is its appearance as an early ontogenetic state in many frogs.

Contrary to Inger's (1967) contention, the available evidence points to the primitiveness within the Anura of the notochordal state of the vertebrae of *Leiopelma* and *Ascaphus*. The sequence in which organs appear during the ontogeny of an animal does not constitute evidence for the early or late appearance of these organs during the animal's evolutionary history as organs which are known to have arisen relatively late in phylogeny often appear early in ontogeny and *vice versa* (de Beer, 1958). The state of the vertebrae of the Lepospondyli is also irrelevant as the Anura are generally considered to have evolved from labyrinthodonts, either independently or together with the Urodela and Apoda (see Romer, 1968). A current view is that all three orders of living amphibians evolved from labyrinthodonts belonging to the Dissorophoidea (Bolt, 1969).

Within the Amphibia as a whole, persistence of an uninterrupted notochord in the adult vertebral column is more primitive than its partial or complete absence because an uninterrupted notochord was inherited by labyrinthodonts from their rhipidistian ancestors (Romer, 1966). In any smaller group within the Amphibia such as the Anura, the presence of an uninterrupted notochord in adult stages may be this original amphibian character-state retained in living forms, or it may have arisen secondarily as a result of neoteny, especially as heterochrony appears to be widespread among frogs (E. M. Stephenson, 1960, 1961; N. G. Stephenson, 1965; Jacobson, 1968).

Pre-anuran fossils do not resolve this point because only one extinct amphibian is known which is structurally intermediate between Palaeozoic tailed amphibians and the Anura, namely *Triadobatrachus massinoti*. Contrary to the opinion of most authors, including Piveteau (1937, 1955) and Watson (1940), who considered *T. massinoti* to have been adult, Griffiths (1956, 1963) claimed that it was an immature animal comparable to living frogs during metamorphosis. There is also uncertainty as to the structure of its vertebrae. According to Piveteau (1937) they are cylindrical, amphicoelous, with a medial constriction, and separated from one another by a lens of cartilage. Griffiths (1963) re-examined the specimen and described its vertebral column as a chain of bony, spool-shaped centra, pierced by a persistent notochord, and without any evident emargination on either their anterior or posterior borders. The difference between these two descriptions concerns the continuity or otherwise of the notochord throughout the column and the nature of the material between consecutive vertebrae. From Piveteau's (1937, 1955) photographs of the fossil, it is clear that ball and socket joints are not present between consecutive vertebrae and that the ends of the vertebral bodies, particularly those lying between the ilia of the pelvic girdle, contain conical plugs of matrix (see also Hecht, 1962). Whether this matrix has replaced notochordal tissue or cartilage is unknown. From Piveteau's photographs it is impossible to decide whether the vertebrae of *T. massinoti* were solid, holochordal elements joined together by imperforate lenses of intervertebral cartilage, or whether they were hollow and ectochordal with the notochord strongly constricted between the vertebrae by the intervertebral cartilage as in *Ascaphus* and *Leiopelma* or unconstricted as in some apodans and urodeles (see Mookerjee, 1930; Hilton, 1948; Lawson, 1966; Wake, 1970).

Even if the structure of the vertebrae of *T. massinoti* could be determined with certainty, its bearing on the vertebral morphology of living frogs is questionable. In the first place, although *T. massinoti* is structurally intermediate in many of its skeletal characteristics between Palaeozoic amphibians and the Anura, it was not necessarily ancestral to the Anura (*cf.* the relationship between the Jurassic Ardeosauridae and the Recent Gekkonidae—Moffat, 1972).

Therefore it cannot be assumed that the various types of vertebrae found in living frogs have necessarily evolved from that found in *Triadobatrachus*. In the second place, if Griffiths' (1956, 1963) contention that *T. massinoti* was an immature animal is correct, it cannot be assumed that the condition of its vertebrae is primitive in the Anura, although this may be the case. It is the state of the vertebrae in the adult animal which shows the stage reached by this animal in the evolution of vertebral structure in the group to which the animal belongs. In any case, as the amount of bone in the skeleton of *T. massinoti* is comparable to that in adult anurans rather than metamorphosing stages where the skeleton is still largely cartilaginous (see Parker, 1881), it would appear that *Triadobatrachus* was in fact an adult animal representing an early stage in the evolution of the Anura.

Fossil frogs belonging to the genus *Notobatrachus* from the Jurassic of Patagonia (Reig, 1957) provide some evidence for the primitiveness of notochordal vertebrae in the Anura. According to Reig, the vertebrae of *Notobatrachus* have the same form as those of *Leiopelma* and *Ascaphus*; he described biconcave centra and unossified intercentra (*i.e.* intervertebral cartilages), while his figures 6 and 7 show the presence of a slender notochordal canal in the ends of the vertebrae. Although it cannot be assumed that *Notobatrachus* was directly ancestral to any group of living frogs, including *Leiopelma* and *Ascaphus*, with which some authors consider it to be confamilial (*e.g.* Griffiths, 1963), the existence of a persistent notochord in its vertebrae and the absence of ball and socket articulations between them demonstrate that the type of vertebral construction found in *Leiopelma* and *Ascaphus* is not a recently acquired condition but existed in the earliest known members of the Anura.

Although the structure of the vertebrae in adult *Leiopelma* and *Ascaphus* bears a superficial resemblance to that found in immature stages of other living frogs with holochordal vertebrae such as *Bufo melanostictus* and *Rana temporaria*, the differences between them are significant (see also Ritland, 1955). In metamorphosing *B. melanostictus* and *R. temporaria* only 9 mm and 12 mm respectively in total length the ball and socket joint between the vertebrae has already begun to develop, the notochord consists only of notochordal tissue and is of uniform width in horizontal sections except for the narrow region between the vertebrae, where it is constricted by the ring of intervertebral cartilage (Mookerjee, 1931, Pl. 15, fig. 8; Pl. 16, fig. 12). In adult *Ascaphus* and *Leiopelma* there is no sign of an incipient joint within the intervertebral cartilage, the constricted portions of the notochord are fibrous and its relatively unconstricted portions occur only in the centres of the vertebrae. Therefore the state of the vertebrae in adult *Ascaphus* and *Leiopelma* is not the same state as that found in juvenile *Bufo* and *Rana* and consequently cannot be considered neotenic compared with the adult condition in the last-named genera.

In some families of frogs, such as the Australian Leptodactylidae, the procoelous holochordal vertebrae do not develop by the invasion of an arc of connective tissue into the intervertebral cartilage as in *Bufo* and *Rana* (Mookerjee, 1931) but by the fusion of a free intervertebral disc to the posterior end of the preceding vertebra (N. G. Stephenson, 1965). Stephenson maintained that within the Leptodactylidae heterochronous changes have been responsible for many of the morphological differences used to distinguish genera and species and that all stages are found in adult leptodactylids from the completely free intervertebral disc condition to the completely fused procoelous state found in *Cyclorana australis*. A similar range of structure was described by N. G. Stephenson (1965) in other parts of the leptodactylid skeleton. For example, the skull of adult *Glauertia russelli* is similar in structure to that of juvenile *C. australis* in that it is largely cartilaginous and the bony elements are small, delicate structures which in many cases are widely separated from one another,

whereas the skull of adult *C. australis* is heavily ossified with extensive surface sculpturing and many elements are broad plates of bone with extensive sutures between them. If adult *Leiopelma* and *Ascaphus* were neotenic compared with other frogs such as *Rana temporaria* in the way that *Glauertia russelli* is neotenic compared with *Cyclorana australis*, one would expect this to be evident in their cranial morphology. In fact, the amount of bone in the skull of *Leiopelma hochstetteri* (E. M. Stephenson, 1951, fig. 16) and *Ascaphus truei* (Noble, 1931, fig. 81) is of approximately the same order as that found in *R. temporaria* (Marshall, 1951, figs 7, 8).

Although it is possible that the presence of an uninterrupted notochord and the absence of ball and socket joints in the vertebral columns of *Leiopelma* and *Ascaphus* could have resulted from some form of heterochrony other than overall neoteny (see de Beer, 1958), the similarity between *L. archeyi* and *L. hochstetteri* in the states of these characters despite heterochronous changes in other parts of the skeleton (see E. M. Stephenson, 1960) suggests that the internal morphology of the vertebral column of *Leiopelma* is not affected by heterochrony. Furthermore, although the vertebrae of *Ascaphus* as illustrated by Ritland (1955) are more heavily ossified than those of *Leiopelma*, constriction of the notochord is no greater than in *Leiopelma*.

From the foregoing discussion it would appear that the presence of an uninterrupted notochord and the absence of ball-and-socket joints in the vertebral columns of *Leiopelma* and *Ascaphus* are not secondarily derived conditions resulting from neoteny as postulated by Inger (1967) but ancestral conditions which have been retained in living forms and which are therefore primitive character-states within the Anura. Whether the type of vertebra found in these two genera could have been ancestral to all other types of anuran vertebrae, however, has yet to be established. The principal ontogenetic changes required to derive the type of holochordal vertebrae found in *Bufo* and *Rana* (see Mookerjee, 1931) are the invasion of the intervertebral cartilage by an arc of connective tissue to form the ball-and-socket joints and more extensive ossification to obliterate the notochord within the vertebra. Atrophy of the notochord and ventral portions of the perichordal tube, including the presacral subchordal cartilage in *Xenopus* (Mookerjee, 1931; Smit, 1953) produces the stegochordal condition (Griffiths, 1959b, 1963). From Mookerjee's (1931) account and the present description of vertebral development in *Leiopelma*, it is clear that the critical stages in ontogeny which determine the adult state of the vertebrae in these frogs occur during or immediately after metamorphosis, even in frogs like *Rana temporaria* which take several more years to complete development. It is not possible to comment here on the possible course of evolution of the holochordal procoelous vertebrae of the Leptodactylidae because, although it is known that the condyles of the vertebrae are formed by the fusion of free intervertebral discs (N. G. Stephenson, 1965), other aspects of the ontogeny of leptodactylid vertebrae are unknown. According to Griffiths (1959b, 1963), the free disc condition in the Megophryinae and some members of the Criniainae is not the developmental precursor of procoelous or opisthocelous vertebrae but is the end product of a particular type of vertebral development.

Two other aspects of vertebral development and adult structure in *Leiopelma* require further discussion, namely the occurrence of ribs and the construction of the sacrum and urostyle.

Ribs

The presence of ribs in association with the third and fourth vertebrae of *Ascaphus* and *Leiopelma* has long been recognized (Noble, 1931; E. M. Stephenson, 1952, 1960; Ritland, 1955) but the laterally directed processes without sutures borne by other vertebrae are usually described as transverse

processes or diapophyses, thus implying that they consist entirely of outgrowths from the neural arches. From the present study it is clear that all these processes including those of the sacral vertebra, whether or not they possess a suture in adult stages, are formed in part from tissue originating outside the vertebra and are therefore pleurapophyses (see Cligny, 1899*a*, 1899*b*; Hofstetter, 1939; Smit, 1953). N. G. Stephenson (1965) pointed out that the terminal cartilaginous epiphyses of the pleurapophyses which are found in leptodactylids as well as many other frogs including *Ascaphus* and *Leiopelma* presumably represent the cartilaginous sternal (*i.e.* distal) portions of the ribs of other tetrapods.

According to Piveteau (1937), the forked ribs of the third vertebra in *Ascaphus* and *Discoglossus* enclose the anterior lymph hearts. Ritland (1955) disagreed with Piveteau and claimed that the large ribs of the third and fourth vertebrae, one pair of which may be forked, provide origins for muscles inserting on the scapula and suprascapula of the pectoral girdle. In *Leiopelma* the forked ribs also have muscles attached to them but they are also closely associated from early stages with thin-walled vessels which are usually empty of cellular material but sometimes contain erythrocytes. These vessels are evidently the anterior lymph hearts described by Piveteau (1937) and the occasional presence of erythrocytes in them is explained by the ability of lymph vessels to return extravasated erythrocytes to the blood vascular system (Le Gros Clark, 1965). In early embryos the dorsal components of the pectoral girdle are widely separated from the ribs and lymph hearts but by the third week after hatching. *i.e.* during metamorphosis, the suprascapula has grown over the ends of the pleurapophyses so that each lymph heart is enclosed in a channel whose floor and inner wall are formed by the two rami of the pleurapophysis and whose roof is the suprascapula (Plate XI (J)).

Development of Urostyle

The urostyle of adult anurans represents the proximal region of the postsacral (caudal) axial skeleton after atrophy of the embryonic or larval tail during metamorphosis. Its structure and development in a variety of frogs have been described by many authors including Ridewood (1897), Gadow (1897), Schauinsland (1906), Mookerjee (1931), Mookerjee and Das (1939), Hodler (1949*b*), E. M. Stephenson (1952), Smit (1953), Stokely and List (1955), van Dijk (1960) and Griffiths (1963), many of whom have given comprehensive reviews of the previous literature. The main points of disagreement regarding the structure of the urostyle concern the number of vertebral elements contributing to its formation and their relationship with the hypochord. Both these points can be clarified with respect to *Leiopelma*, bearing in mind that the situation in other frogs, particularly those with stegochordal presacral vertebrae, is not necessarily the same.

In the past there were basically three opinions regarding the construction of the urostyle. According to Gadow (1897, 1933) and Romer (1945, 1962, 1966), the urostyle results from the fusion of as many as 12 vertebrae, while Noble (1931) and Shumway (1942) maintained that it is formed by the fusion of three longitudinal, unsegmented strips of cartilage. The third school of thought now appears to be correct, that the urostyle of anurans consists in part of an unsegmented rod which lies ventrally to the notochord and which eventually fuses with several anterior postsacral neural arches (Mookerjee, 1931; MacBride, 1932; Mookerjee and Das, 1939; Smit, 1953; Stokely and List, 1955; Griffiths, 1963).

In developing *Leiopelma archeyi* the ventral component of the urostyle is a rod of cartilage formed from the ventral part of the postsacral perichordal tube which has increased in thickness due to hyperplasia of the chondrified squamous

cells comprising it and their subsequent metaplasia into hyaline cartilage. It occupies the full width of the notochord and, towards the end of metamorphosis, fuses with the bases of the postsacral neural arches and the tracts of cartilage connecting them. The ventral component of the urostyle of *Ascaphus* is formed in the same way as a rod of cartilage within the perichordal tube (Eaton, 1959). In the trunk of *Xenopus laevis* tadpoles there is also a subchordal rod of cartilage which forms from the ventral region of the perichordal tube, but it is resorbed together with the notochord during metamorphosis (Ridewood, 1897 ; Mookerjee, 1931 ; Smit, 1953).

The question arising here is whether the subchordal rod of cartilage in the postsacral region of *Leiopelma* and *Ascaphus* should be described as a hypochord. According to Mookerjee (1931), the rod of cartilage in the trunk of *Xenopus* is not homologous with the hypochord in the tail because the latter is not part of the perichordal tube but a separate structure fused to its ventral surface. A separate hypochord has been described in a number of other anurans and, according to Mookerjee and Das (1939), its relationship with the perichordal tube varies in different species. In *Rana afghana*, *Microhyla rubra*, *Rhacophorus maculatus* and *Xenopus laevis* there lies between the membranous ventral portion of the perichordal tube and the cartilaginous hypochord a continuous band of hyaline cartilage which subsequently degenerates, together with the notochord when the hypochord fuses with the postsacral neural arches and the dorsal region of the perichordal tube to form the urostyle. According to Mookerjee and Das (1939), the band of hyaline cartilage is absent in other anurans such as *Bombinator igneus* so that the hypochord rests directly on the membranous perichordal tube while in others again such as *Rana temporaria* and *Bufo melanostictus* the entire perichordal tube in the region of the urostyle chondrifies but remains distinct from the hypochord even when subsequent ossification of the urostyle is well advanced (Mookerjee, 1931, Pl. 15, Fig. 10 ; Mookerjee and Das, 1939, Fig. 12B). The separate identity of the hypochord in the pelobatid *Megophrys major* is particularly clear because metamorphosing stages of this frog have approximately 17 ossified caudal vertebrae of which the most anterior four are attached to the dorsal surface of the cartilaginous hypochord (Griffiths, 1956, 1963).

Although the separate identity of the hypochord is usually established from its manner of origin during ontogeny, this seems to be as variable as the later relationship of the hypochord with the overlying perichordal tube. From the works of Mookerjee (1931) and Smit (1953) it appears that the hypochord of *Rana temporaria*, *Bufo melanostictus*, *Bombinator igneus* and *Xenopus laevis* originates as a longitudinal condensation in the subvertebral mesenchyme which subsequently chondrifies. Stokely and List (1955) described the hypochord in *Pseudacris nigrita* during metamorphosis as an ossified rod-like process but concluded that the exact origin of the hypochord during ontogeny has yet to be determined. Griffiths (1963) described the hypochord of *Megophrys major* as a posterior, ventral outgrowth of the first postsacral intervertebral body and implied that it arises in this manner in all anurans. Despite this diversity of opinion and the diversity it suggests regarding the origin of the hypochord in different members of the Anura, it would appear that the separate hypochord in many species has no counterpart in *Leiopelma* and *Ascaphus* whose subchordal rod of cartilage is part of the perichordal tube. Nevertheless the subchordal rod of *Leiopelma* and *Ascaphus* may be considered homologous with the hypochord of other anurans since they are both rods of cartilage which lie ventrally to the postsacral notochord and constitute the ventral component of the urostyle. According to Szarski (1962), organs which have the same structure and the same location in relation to neighbouring organs are homologous, although they may develop in very different ways.

The number of postsacral vertebral segments involved in the formation of the urostyle has also been debated, largely because discrete caudal vertebrae are rarely found in anurans. To date, *Megophrys major* described by Griffiths (1956, 1963) appears to be the only exception in that metamorphosing stages have approximately 17 ossified caudal vertebrae, of which the first four contribute to the urostyle. In embryonic and recently hatched *Leiopelma archeyi* there are usually fourteen pairs of neurapophyses in all, less often fifteen. As the tenth pair is usually sacral and the specimens with fifteen pairs had the eleventh vertebra modified to support the pelvic girdle, it would appear that four pairs of postsacral neurapophyses are normally present during developmental stages. In the adult specimen of *L. archeyi* examined, only three pairs of postsacral neurapophyses were present, which suggests that the tiny fourth pair belonging to the fourteenth vertebra had been indistinguishably incorporated into the urostyle. E. M. Stephenson (1952) maintained that no more than three postsacral vertebrae are normally found in developing *L. hochstetteri*, while her illustration of a common condition of the anterior urostyle of adults (1952, Fig. 2) shows only two postsacral arches. Three pairs of postsacral neurapophyses were present in the adult *L. hochstetteri* examined here, but this specimen was atypical in possessing a free postsacral vertebra. In these circumstances it would appear that *L. archeyi* normally has one more neural arch on the anterior end of the urostyle than *L. hochstetteri* and that in both species the most posterior arch is indistinguishable in adults.

In view of the small size of the most posterior pair of neurapophyses, the number of arches recognizable during developmental stages of *Leiopelma* may not represent the total number of vertebral segments incorporated into the urostyle. The total number of segments can be determined, however, from the relationship between the subchordal rod of hyaline cartilage and the spinal nerves. In late intracapsular and hatching stages of *L. archeyi* the anterior and posterior limits of the rod are ill-defined but, by three weeks after hatching, at a stage comparable to late metamorphosis in other frogs, it terminates abruptly just behind the vent. As the specimen at this stage examined here had a total of fourteen neural arches, the tenth of which was sacral, and the subchordal rod began immediately behind the sacral vertebra and terminated in the region of the sixteenth pair of spinal nerves, it is evident that the most anterior five postsacral vertebrae formed the urostyle and that the fifth of them lacked a neural arch. The dorsal components of this vertebra are the posterior extensions of the tracts of cartilage situated dorsolaterally to the notochord and connecting the bases of the more anterior postsacral arches. Whether the urostyle of *L. hochstetteri* also comprises five vertebrae could not be determined from the material available.

According to van Dijk (1960), the eleventh, twelfth, thirteenth and possibly the anterior half of the fourteenth vertebrae contribute to the formation of the urostyle in *Ascaphus*. van Dijk based this conclusion on the relationships of the coccygeal lymph hearts and the origin on the urostyle of the *pyriformis* muscle in an adult specimen and a larva with well developed hind limbs. He also claimed that Ritland's (1955) identification of a thirteenth spinal nerve in *Ascaphus* suggests the participation of the eleventh, twelfth and thirteenth vertebrae in its urostyle. From this investigation of *Leiopelma* it is seen that the number of spinal nerves associated with the anterior end of the urostyle in fully metamorphosed frogs can show the minimum number of vertebrae present but gives no indication of the total number involved. In embryonic *L. archeyi* the spinal cord and its associated nerves are present throughout the tail but in adults all but the most anterior three postsacral nerves have been resorbed and the spinal cord posterior to the last of the persistent nerves, *i.e.* the thirteenth, is reduced to a slender ependymal tube extending along the dorsal surface of the urostyle to its posterior extremity. As each spinal nerve lies anterior to the

vertebra of the same number, the presence of the thirteenth spinal nerve in adult *L. archeyi* gives no indication that the fourteenth and fifteenth vertebrae are present in the urostyle.

van Dijk (1960) commented on the extreme elongation of the urostyle in *Ascaphus* behind the thirteenth spinal nerve and concluded that the thirteenth vertebra extends almost as far as the position at which the fifteenth should lie due to posterior movement of both the ischiopubic region of the pelvic girdle and the posterior end of the urostyle relative to the sacrum. Similar elongation of the urostyle also occurs in *Leiopelma archeyi* but in this case it applies to the fifteenth vertebra. In the specimen three weeks after hatching which was sectioned transversely at 10 μ , it was calculated that all five urostylar vertebrae were the same length, i.e. 0.27 mm. It was also calculated that the presacral column in this specimen measured 2.62 mm and was therefore almost twice as long as the urostyle. As the urostyle of the adult *L. archeyi* sectioned horizontally was the same length as the presacral column, i.e. 6.8 mm, it is clear that the urostyle has not only increased in length by almost 5.5 mm to become five times its original length but has also grown much more rapidly than the presacral column. As the proportions of the anterior end of the urostyle in postmetamorphic *Leiopelma* do not seem to alter with age (see E. M. Stephenson, 1960, Fig. 3), most of the elongation of the urostyle takes place at its posterior end in the region of the fifteenth vertebra. Moreover, the presence of cartilage at the posterior end of the urostyle of adult *Leiopelma* shows that its growth may continue after sexual maturity.

Evolution of Anuran Pelvis

According to van Dijk (1960), the backward migration of the end of the urostyle and the ischiopubic region of the pelvic girdle rather than a forward migration of the sacro-iliac articulation accounts for much of the forward slope of the ilia in *Ascaphus* and therefore a primitively vertical pelvic girdle would have articulated with a sacrum not more than two vertebrae further back than at present. From the ontogenetic development of the pelvis and sacrum in *Leiopelma*, it is clear that backward migration of the posterior parts of the pelvis and urostyle in postmetamorphic stages accounts for the disproportionately long pelvic girdle in adult frogs compared with non-anuran amphibians, living and extinct (see Smith, 1927; Hilton, 1945-47; Wake, 1963; Romer, 1966), but plays no part in determining the position of the sacrum. This is determined during metamorphosis, before the posterior end of the urostyle is clearly defined, by the growth of the ilia towards the vertebral column, the sacral vertebra being the one whose pleurapophyses are induced to enlarge by the proximity of the anterior ends of the ilia (Ridewood, 1897). The growth of the ilia in an antero-dorsal direction is demonstrated by the movement of their anterior extremities from a position below and behind the pleurapophyses of the eleventh vertebra in hatching stages (Fig. 3) to a position slightly above and in front of the pleurapophyses of the ninth vertebra three weeks after hatching, the tenth vertebra by this stage having become the sacrum (Fig. 7). As the acetabula are situated ventrally to the thirteenth vertebra in both these stages, the posterior migration of the ischiopubic region characteristic of later stages has not yet begun, so that the increase so far in the length of the ilia is due entirely to the growth of their anterior ends in an antero-dorsal direction.

Slight changes in the rate and direction of growth of the ilia and of the more posterior pleurapophyses of the vertebral column during this period could account to a large extent for the different positions of the sacrum in anurans and the different numbers of vertebrae comprising it. Another factor which may alter the position of the sacrum is a shift of the entire pelvic girdle anteriorly or posteriorly along the body as indicated by the position of the acetabulum during

early metamorphosis. Developmental changes of this nature can not only explain the variability of the presacral and sacral regions within species (see Ridewood, 1897) but can also account for the different numbers of presacral and sacral vertebrae which are typical of different species, and which vary between the nine presacrals and one sacral normally found in *Ascaphus* and *Leiopelma* (E. M. Stephenson, 1952 ; Ritland, 1955) to the six presacrals and three sacrals of the brachycephalid *Oreophrynella quelchii* (Noble, 1931). Although occasional specimens of *Leiopelma*, *Ascaphus* and some other frogs such as *Xenopus* have one more than the number of presacral vertebrae typical of the species concerned (Hodler, 1949b ; E. M. Stephenson, 1952 ; Ritland, 1955), it is generally agreed that the overall evolutionary trend in the Anura is towards further shortening of the presacral column as a result of forward migration of the sacro-iliac articulation (Gadow, 1901 ; Green, 1931 ; Ramaswami, 1933 ; Ritland, 1955).

Although anterior migration of the sacro-iliac articulation in the Anura can result from an anterior shift in the position of the pelvic girdle and/or anterior growth of the ilia, it is apparent that only the first of these alternatives could have led to reduction of the presacral column in the ancestors of the Anura. Among the Palaeozoic rhachitinous labyrinthodonts belonging to the Dissorophioidea, which are currently considered to contain the ancestors of the three living amphibian orders (Bolt, 1969), the number of presacral vertebrae varied between eighteen and twenty-six and the pelvic girdle had the robust, plate-like construction and the vertical ilium characteristic of early amphibians (Watson, 1940 ; Gregory, 1950 ; Carroll, 1964 ; Bolt, 1969). As relative changes in the rate of elongation of a vertical ilium would not alter its position on the vertebral column, variation in the number of presacral vertebrae in the Dissorophioidea must have resulted from shifts in the position of the entire girdle. The pelvic girdle of the Triassic pre-anuran *Triadobatrachus massinoti* is structurally intermediate between those of the Dissorophioidea and the Anura in that approximately six caudal vertebrae are present instead of a urostyle, the acetabula lie below the eighteenth vertebra, the fifteenth and possibly the sixteenth vertebrae are sacral and the ilia, although directed anteriorly, are shorter and stouter than those of adult frogs (see Piveteau, 1937 ; Hecht, 1962). Although it is not certain whether *T. massinoti* was a sexually mature adult or a metamorphosing juvenile, it is evident from the relative positions of the sacral ribs, the anterior ends of the ilia, the caudal vertebrae and the acetabula that posterior migration of the ischio-pubic region has not taken place and that the position of the sacrum has been determined little if at all by anterior growth of the ilia.

The sacral vertebra of living anurans varies considerably in external form, not only in the nature of its articulations with the presacral vertebra and the urostyle (see Griffiths, 1963) but also in the shape of its pleurapophyses, which may be of almost uniform width throughout their length as in *Rana* (Noble, 1931 ; Ramaswami, 1933), or slightly expanded as in *Leiopelma* and *Ascaphus* (E. M. Stephenson, 1952, 1960 ; Ritland, 1955) or broadly expanded distally as in other anurans including *Scaphiopus* and *Xenopus* (Noble, 1931). According to E. M. Stephenson (1952, 1960) the sacral vertebra of *Leiopelma* appears to be unique in the Anura because the bony neural arches are joined together dorsally and ventrally by cartilage and the vertebra as a whole is narrower from front to back than the presacral vertebrae. The sacral vertebra of *Ascaphus* as described by Ritland (1955) is fully ossified and of normal size comparable to that of *Discoglossus*. In horizontal section the sacral vertebra of *Ascaphus* (Ritland, 1955, Fig. 3A) resembles the presacral vertebrae in that the mesial surfaces of the neural arch bases lie close to the surface of the unconstricted notochord, whereas horizontal sections of *Leiopelma* (Fig. 9) show the arch bases to be widely separated from the surface of the notochord which has become greatly constricted by hyperplasia of the perichordal tube within the vertebra. Whether the marked

difference seen here between the sacral vertebrae of *L. archeyi* and *L. hochstetteri* is of normal occurrence could not be determined from the material available but, of these two specimens, the sacral vertebra of *L. archeyi* more closely resembles the presacral vertebrae in the size of the arch bases and their relationship to the perichordal tube than does the sacral vertebra of *L. hochstetteri*.

From E. M. Stephenson's (1952, 1960) descriptions and illustrations of the sacral vertebra in *Leiopelma*, its failure to fuse ventrally appears to be due to the absence of a centre of ossification between the arch bases like those of the more anterior vertebrae. However, the atlas also lacks a mid-ventral centre of ossification (E. M. Stephenson, 1960, Fig. 3), yet this vertebra becomes enclosed in bone in later stages, apparently due to ventral growth and subsequent fusion of the bone of the neural arches. As the sacral vertebra fails to ossify dorsally and ventrally even in comparatively aged specimens in which the mid-dorsal cartilage has calcified (E. M. Stephenson, 1960), it would appear that the persistence of cartilage mid-dorsally and mid-ventrally in this vertebra has not resulted simply from delayed development of the vertebra but has instead been selected for because of its functional significance. It probably serves as a shock-absorber to reduce jarring of the axial skeleton during saltatorial locomotion, especially as the ligamentous connection between the ilia and the sacral pleurapophyses appears to be a firm one (E. M. Stephenson, 1952). According to Ridewood (1897), a close connection between the ilia and sacrum such as that found in "the frog" (presumably *Rana* sp.) is rare in anurans, the majority of which have considerable mobility of the ilia relative to the sacrum, especially those genera with broadly expanded sacral pleurapophyses. In terrestrial anurans, mobile sacro-iliac articulations would act as shock-absorbers, but in some aquatic forms such as *Pipa* and *Xenopus* the extreme mobility of these joints is an adaptation to allow rapid elongation of the body to dilate the pharynx for the rapid engulfment of food (Willem, 1939).

Relationship between Leiopelma and Ascaphus

The vertebral morphology of *Ascaphus* and *Leiopelma* is not indicative of close relationship between them. Although the persistence of a continuous notochord in adult stages and the absence of synovial joints between the bodies of consecutive vertebrae are character-states found only in these two genera of anurans, they have been shown already to be character-states inherited from the ancestors of the Anura and could therefore have persisted independently in distantly related genera. Although the moniliform configuration of the notochord is similar in *Ascaphus* and *Leiopelma*, it results from greater constriction between vertebrae than within them due to centripetal growth of the intervertebral cartilage, and centripetal growth of the intervertebral cartilage also occurs in other anurans which acquire synovial intervertebral joints such as *Rana temporaria* (Mookerjee, 1931). Other vertebral characteristics, on the other hand, such as the continuous fibrous core of the notochord in *Ascaphus* and the structure of the sacral vertebra in *Leiopelma*, as well as other differences between the two genera reported by Noble (1931), E. M. Stephenson (1951), N. G. Stephenson (1951*b*), Stephenson, Robinson and Stephenson (1972) and Robinson, Stephenson and Stephenson (1973) strongly suggest that *Ascaphus* and *Leiopelma* are not sufficiently closely related to be placed in the same family (see Kuhn, 1967; Fawcett and Smith, 1971).

In view of the number of character-states shared by *Ascaphus* and *Leiopelma* which appear to be primitive states in anurans generally (Howes, 1888; Noble, 1931; de Villiers, 1934*a*, 1934*b*; Pussey, 1943; E. M. and N. G. Stephenson, 1947; N. G. Stephenson, 1951*b*, 1965; Szarski, 1951; E. M. Stephenson, 1951, 1952, 1955, 1960; Ritland, 1955; Griffiths, 1963), it would appear that these two genera are both relics of ancient but otherwise independent groups within

the Anura. Further support for this contention is provided by the presence of additional primitive character-states in one genus or the other, such as the well-developed abdominal ribs of *Leiopelma*, traces of which also appear in the discoglossid *Bombina* but which are absent from *Ascaphus* (Noble, 1931; E. M. Stephenson, 1952, 1960).

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EXPLANATION OF PLATES

Abbreviations: *a*, atlas; *alh*, anterior lymph heart; *cart*, cartilage; *fc*, fibrous cartilage; *g*, ganglion of 13th spinal nerve; *il*, ilium; *ivc*, intervertebral cartilage; *my*, myotome; *ms*, marrow space; *n*, *na*, neurapophysis or neural arch; *nab*, base of neural arch; *nal*, lamina of neural arch; *nc*, notochord; *ncs*, notochordal sheath; *occ*, occipital condyle; *pb*, perichondral bone; *pct*, perichordal tube; *plp*, pleurapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis; *r*, rib; *sc*, spinal cord; *scp*, suprascapula; *scr*, subchordal rod; *sg*, spinal nerve ganglion; *sg9*, *sg11*, *sg16*, *sg18*, ganglia of 9th, 11th, 16th and 18th spinal nerves; *sn13*, 13th spinal nerve; *snab*, base of sacral neural arch; *splp*, sacral pleurapophysis; *trp*, transverse process; *u*, urostyle; *V5*, *V9*, 5th and 9th vertebrae; *zb*, zygapophyseal bar.

PLATE IX

Vertebrae of intracapsular embryos of *Leiopelma archeyi* in transverse section. A. Mid-trunk vertebra of a Stage 2 embryo. Van Gieson. B.-G. Stage 3 embryo. Azan. B. Region between bases of atlantal neurapophyses and occipital region of chondrocranium. C. Posterior region of neural arch base of second vertebra showing its relationship to the perichordal tube and the notochord. D. Third vertebra showing relationship between neurapophysis, mesenchymatous rib and anterior lymph heart. E. Seventh vertebra with mesenchymatous rib. F. Intervertebral region between eighth and ninth vertebrae. Note mesenchymatous zygapophyseal bar. G. Eleventh vertebra. The single arrow in E and G indicates cells migrating from the dorsal extremity of the myotome to the dorsal region of the neurapophysis.

PLATE X

Axial skeleton of late intracapsular embryos of *Leiopelma archeyi*. A and B, Stage 4, L. S. Azan. A. Developing atlanto-occipital joint. B. Procartilaginous zygapophyseal bar between fourth and fifth vertebrae. C.-F. Stage 5. C. Tenth vertebra with mesenchymatous rib. T. S. Azan. Migration of cells from dorsal extremity of myotome to neurapophysis is indicated by the double arrow. D. Eleventh vertebra with mesenchymatous rib and mid-ventral hyperplasia of perichordal tube. T. S. Azan. E. Cartilaginous zygapophyseal bar between fifth and sixth vertebrae. Oblique H. S. Masson. F. Posterior trunk and anterior tail. Note tract of cartilage, *cart*, along dorsolateral surface of notochord. Oblique H. S. Masson. The single arrow in A, B and E points anteriorly.

PLATE XI

Vertebrae of *Leiopelma archeyi* at hatching (Stage 6) and three weeks after hatching (Stage 9) in transverse section. Azan. A.-F. Stage 6. A. Cartilaginous rib of third vertebra showing its relationship to the transverse process of the neural arch and the anterior lymph heart. B. Cartilaginous rib and transverse process of fourth vertebra. C. Mesenchymatous rib of eleventh vertebra. D. Twelfth vertebra with mesenchymatous rib and subchordal rod. E. Thirteenth vertebra with mesenchymatous rib and subchordal rod. F. Oblique T.S. of fourteenth vertebra showing maximum height of neural arch on the left and the tract of cartilage joining the bases of the neural arches on the right. Limits of perichordal tube are ill-defined. G.-L. Stage 9. G. Developing atlanto-occipital joint. H. Developing zygapophyseal joint between third and fourth vertebrae. J. Anterior lymph heart lying between pleurapophysis of third vertebra and suprascapula. K. Pleurapophysis of sixth vertebra showing rib fused to transverse process. L. Ligamentous connection between sacral pleurapophysis and ilium. All figures are to the same scale shown at bottom of plate.

PLATE XII

Urostyle region of *Leiopelma archeyi* three weeks after hatching (Stage 9) and vertebrae of adult *Leiopelma*. A.-E. Developing urostyle in *L. archeyi*, Stage 9. T.S. Azan. A. Eleventh vertebra showing fusion of subchordal rod to neural arch bases and constriction of notochord. B. Thirteenth vertebra. C. Subchordal rod and tracts of cartilage on dorsolateral surfaces of notochord posterior to 14th pair of spinal nerves. D. Posterior end of subchordal rod immediately anterior to 16th pair of spinal nerves. E. Axial skeleton of tail immediately posterior to end of subchordal rod and 16th pair of spinal nerves. F.-J. Vertebrae of adult *Leiopelma*. H.S. F. Atlanto-occipital joint of *L. hochstetteri*, showing fibrous cartilage in the notochordal canal in the anterior end of atlas and the posterior region of the *basis cranii*. Masson. G. Mid-trunk vertebrae of *L. hochstetteri*. Masson. Only the right side of the column is shown. H. Mid-vertebral and intervertebral regions of the notochord in the trunk of *L. archeyi*. Mallory. J. Posterior trunk vertebrae, sacral vertebra and anterior urostyle of *L. archeyi*. Mallory. The arrow accompanying figures F.-J. points anteriorly.

